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THE BOTANICAL REVIEW

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SELECTIVE BREEDING OF SUGAR-BEETS IN RUSSIA AND THE U.S.S.R.

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Background and Organization of the Industry

FOUNDING AND DEVELOPMENT UP TO THE REVOLUTION

Sugar-beet selective breeding in Imperial Russia was started somewhat later in the nineteenth century than in Germany, France and other western European countries. The expanding industry which depended on this crop in Russia at that time demanded large quantities of seed, and this need was at first fulfilled by importation of seed from German and French seed companies: Rabbethge und Giesecke, Dippe, Vilmorin and others. Because the imported seed was expensive, locally grown foreign seed stock became very popular. Gradually the country developed its own sugar-beet selective breeding stations. Up to the 1880's breeding work consisted of selection on the basis of the external appearance of plants (morphological selection) or on the specific gravity of the roots. By the end of the 1880's and in the 1890's, the better selection stations were changing over to individual and family selection by polarimeter measurements.[2] Zalenski (85) states that selection laboratories were set up by the hundreds toward the end of the 1890's, and that millions of beet roots were examined with polarimeters. Many of the stations existed only a short time, but just before World War I there were 42 in operation (85) [3]. Many of the breeders who worked at these stations published the results of their scientific work in Russian and in foreign periodicals [4].

The results of the serious selective breeding work were immediate. From 1891 on, the sugar-beet branch of the Warsaw division of the Society for the Promotion of Russian Industry and Trade began to conduct tests of the sugar-beet varieties produced by the selective breeding stations as well as by foreign seed companies.

[2] For example, the advertisements of the selection station belonging to Count V. Tyshkevich indicated that Pellets' method was introduced in 1892, with the participation of the inventor himself.

[3] Some of these were the following:

Station headed by A. Janacz, founded in 1888.
Station headed by Buszczniski and M. Lazynski, founded in 1886.
Station under V. Maisel (1875).
Stations headed by the heirs of A. E. Koenig, Haritonenko, Countess Branitskaya, Count Bobrinsky.
Stations at Uladovka, Verhnyachka, Kalnik, Ilyinitsk, and elsewhere.

[4] Among such contributions are those by Zalenski, E. Kostetski, T. Zalesski, S. Rytel, L. Sempolovski, G. Skrodski, I. Volski, A. Zaikevitch, Trzhebinski, Janacz, Kudelka, Harkevitch and Dzengelevski.

These varietal tests were organized on a strictly scientific basis and were carried out in such a manner as to assure complete impartiality in evaluating the varieties and to avoid any possible bias. The tests showed that varieties bred by the best Polish, Ukrainian and Russian sugar-beet selective breeding stations were equal in quality to the best varieties of foreign companies (85).

The position of many of the selective breeding stations was not an easy one because the cost of breeding work was added in the cost of the seed, and many owners of sugar factories failed to understand the advantages of having good planting varieties at their disposal. Accordingly, some owners of sugar factories and estates began unselected multiplication of commercial seed instead of relying on stocks from selection. Also, numerous seed companies sprang up that released seed which had not been selected or which had undergone very crude methods of selection. These seeds were sold at a low price, and the owners of estates and of sugar factories eagerly bought them. The small saving in cost thus acquired was accompanied by considerable loss for the factories in both yield and quality of the beets raised from them.

Only a few of the factory and estate owners resisted this general trend and continued to use selected seed. Some of the more responsible seed companies could not hold out against competition and had to close; others were compelled to simplify their methods of selection in order to reduce expenses, and in this way lowered the quality of the seed they produced. The decrease in volume of seed production and the closing of some of the local selective breeding stations resulted in an increase of business for foreign companies. This state of affairs was exploited especially by Rabbethge und Giesecke, German seed growers, who arranged for increase of their elite strains of seed in the district of Podolsk in the Ukraine, constructed a large elevator for cleaning and storage of seed at Vinnitza, and moved to first place among producers of sugar-beet seed in Russia.

In addition to breeding and selection work, extensive experimentation was carried on in Russia on the culture and fertilizing of sugar-beets. Between 1900 and 1918, an organization named Network of Experimental Fields, which had been set up by the All-Russian Society of Sugar Factory Owners, was in operation; it comprised 32 experimental fields and several experimental stations.

The contributions by the personnel of the Network—S. L. Frankfurt, S. Tulaikov, A. Dushechkin, A. Nesterov, A. Philippovsky and others—were published in a series of annual reports.

At the Haritonenko estates, annual meetings of estate managers and agronomists engaged in experiments with sugar-beets were organized. At these meetings, scientific reports were presented, and they served to promote advanced agronomic ideas on sugar-beet production. The chairman was Professor D. N. Pryanishnikov, and among the participants were a number of men prominent in experimental work: Kossovich, Zaikevich, Franfurt and others.

Scientific investigations on pests and diseases affecting sugar-beets and methods for their control were chiefly conducted at the entomological station of the All-Russian Society of Sugar Factory Owners in the city of Smela, Kiev district and under the direction of E. Vassil'yev who published annual reports on the work carried on at the station. Another center was a special station in Kiev for the study of plant insect and disease problems, which had been set up by the South Russian Society of the Advancement of Agriculture and Crop Production.

Thus the problems of growing and selective breeding of sugar-beets, and of the pests and diseases of this crop as well as measures for their control were being intensively studied in Russia on the eve of the domestic upheavals brought on by World War I and the Revolution. The war naturally caused many disturbances in scientific research and selection work on sugar-beets. Importation of German seed ceased, and many of the Polish selective breeding stations found themselves in the occupied zone. At the same time the beet-sugar industry in areas that were not occupied by the German armies continued to put forth demands for seed; moreover, Russia became practically the only source of sugar-beet seed for the Allies. For this reason some of the selective breeding stations increased their activity during the war, and many new institutions for sugar-beet selective breeding were started. Advantage was taken of the situation by certain second- and third-grade seed companies that began to produce beet seed by mass propagation without any selection whatever. The seed stocks so produced were sold to the Allies (USA, England, France, Italy, Rumania), and the quality of the seed was very justly criticized. This period of exploiting a world shortage of sugar-beet seed was of short duration.

DISINTEGRATION DURING THE REVOLUTION

The agrarian disorders which occurred during the Revolution brought with them either complete destruction of the selective breeding stations—including buildings, laboratories and stocks of seed—or destruction of laboratory equipment, selective breeding records and archives, a mixing up of selective breeding seed materials, and so on. At the very first opportunity many of the men in charge of research at selective breeding stations moved to Poland to save their lives.[5] Part of the experienced technical staff followed them; the rest scattered in all directions and were lost to the sugar-beet industry. There remained only a few stations where the selective breeding seed material was to some extent preserved, but mostly without records. For the most part the selective breeding work that had started and so greatly expanded before World War I was completely destroyed[6]:

Table I presents the decrease in sugar-beet production in the Ukraine—at first gradual during the war, then reaching catastrophic proportions (18). Toward the end of the war the decrease amounted

TABLE I. PRODUCTION OF SUGAR-BEET SEED IN THE UKRAINE, 1914–1920

Year	Total area planted to beets (in acres)	Average yield of beet seed (in quintals * from 1 acre)	Total harvest of beet seed (in metric tons)
1914	81,000	10.7	39,312
1915	72,000	10.3	32,678
1916	56,700	9.4	22,932
1917	48,600	8.7	18,018
1918	40,500	8.0	14,742
1919	16,200	6.7	4,914
1920	2,700	5.3	650

* One quintal = 100 pounds = 45.4 kilograms.

to one-half, and at the time of greatest destruction during the Revolution to one-thirtieth, as compared with the planted area for 1914. Since there was a drop in yield simultaneously with reduction in acreage, it is not surprising that the total yield of beet seed for 1920 was one-sixtieth of the yield in 1914.

[5] Among the foremost of the Polish breeders were E. Zalenski, E. Kostetzki, S. Rytel, E. Volski, G. Skrodski and Kudelka.

[6] The Uladovka selective breeding station was exceptionally fortunate because it did not suffer destruction, nor were there any changes in personnel; the chief selective breeder, Dr. L. Sempolovsky, remained in charge.

RECONSTRUCTION UNDER THE PLANT VARIETY AND SEED PRODUCTION ADMINISTRATION OF THE SUGAR TRUST

After the Revolution the sugar industry gradually was restored and, of course, required supplies of sugar-beet seed. At first it was still possible to use old seed stocks, but when these were exhausted it became necessary to rebuild the seed industry that had been destroyed. This was the aim of the newly organized Plant Variety and Seed Production Administration of the Sugar Trust ("Sortovodno-Semennoye Upravleniye Sakharotresta"), which was given 12 selective breeding stations that had been destroyed or damaged to vary degrees. At first only a small staff of workers constituted the Administration. There was a gradual increase in the scientific personnel so that by 1927 the central bureau and the selective breeding stations of the Administration consisted of 140 men. For a long time the scientific and technical leader of this complex organization was B. A. Panshin who showed great knowledge of the business and a talent for organization. Unfortunately he was forced to work in an atmosphere of constant and completely undeserved distrust by the Soviet Commissars. He was arrested several times and finally died in exile. A large number of scientific papers came from the pen of Panshin. Among these, special mention should be given to his monograph on sugar-beet breeding (47) and his bibliographical index of literature on sugar plants (48)

The official nominally in charge of the Administration was always a Communist Party leader. Such Party men at first understood very little of the business of the organization under them, but gradually, thanks to constant explanation by the specialists, the Commissars began to understand a little about the technical work at hand. However, in the usual course of events the Party officials would be shifted from their jobs, and the process had to be gone through again.

THE ADMINISTRATION'S SELECTIVE BREEDING STATIONS. At first the Administration devoted most of its attention to the reconstruction and rehabilitation of the selective breeding stations and to reemployment of former members of the personnel of the stations, many of whom were still living in their old homes. The next step was to straighten out the mixed stocks of seed for use in further selection work. Soon the polarization laboratories were set up

again and mass selection of sugar beets was organized. During the winter of 1921–1922, at all selective breeding stations combined, over a million sugar-beet roots were analyzed. Gradually there was a change-over to individual selections, and in 1923 about 2,500 lines from individual selections were being studied at the various stations.

Because of a lack of trained selective breeders for sugar-beets and other crops, university courses on the selective breeding of agricultural plants were organized in 1920 in Kiev.[7] After completion of the courses most of the students were appointed as specialists at selective breeding stations. Each station had its own special field of work and used methods appropriate to the crops assigned: sugar-beets, winter wheat, rye, barley, oats, millet, peas, lentils, etc. By 1923 re-construction was completed. The history of these selective breeding stations and details of their work have been described in a special publication (71).

The Plant Variety and Seed Administration organized scientific meetings periodically, at which personnel of the Administration's central bureau and the selective breeding stations presented papers on scientific, organizational or technical subjects. The papers read at these meetings were usually published in the form of abstracts (76).

A Scientific Council was organized within the Administration. The Council consisted of prominent specialists from the Administration and the selective breeding stations under its jurisdiction; several professors of the Kiev Agricultural Institute; and scientists well known in the fields of genetics, selective breeding and experimental work, for example, academy members Vavilov, Sapegin, Pryanishnikov and Yakushkin.

The selective breeding stations run by the Administration were at first inadequately staffed and unevenly distributed in the beet-growing zone. Seven of them were located in the Kiev district, three in the Podol district, and one each in the districts of Kharkov and Poltava. In two districts (Voronezh and Kursk) where the sugar-beet industry was well developed there were no stations at all. Because of these facts the Administration undertook a reorganization of the network of selective breeding stations in its

[7] The lecturers were Professors Kolkunov, Votchal, Malyushitski, Tabentski, Levitski, Larionov, Yanata, assisted by a number of outstanding agricultural specialists (Panshin, Dushechkin, Gruener, Solyakov, Nevadovski, Dobrovlyanski, Lebedinski, Voitkevich, and others).

care between 1923 and 1933. This reorganization consisted of closing down some of the stations that were located too close to each other and opening up new ones that were badly needed, particularly in the so-called new regions of beet culture. It must be noted, however, that the liquidation of certain of the old stations was often carried out too hastily and carelessly, as a result of which the normal course of selective breeding work was disturbed and selected stocks of seed were lost.

The following network of stations resulted from the reorganization:

Ukraine

Kiev district: Station Byelaya Tserkov, Uladovka, Verkhnyachka.
Vinnitsa district: Nemercha station and the Yaltushkovsk selective breeding point.
Poltava district: Veselo-Podol' station.
Sumsk district: Ivanov station.

Russia (RSFSR) (Russian Soviet Federated Socialist Republic)

Voronezh district: Ramon station.
Kursk district: L'gov station.
Northern Caucasus: *Pervomaiskaya* (May First) station.
Western Siberia: Biisk station.

Kirghiz SSR (Central Asia)

Kirghiz station.

SUPPLYING SUGAR-BEET FACTORIES WITH SEED. To assure uninterrupted operation of sugar factories, about 24,500 metric tons of sugar-beet seed were needed for planting every year. Until 1925 it was never possible to produce the amount required. Table II shows the rate of increase in production of sugar-beet seed from all the planting areas of the Sugar Trust previous to and shortly after that year:

TABLE II. PRODUCTION OF SUGAR-BEET SEED ON SUGAR TRUST AREAS, 1921–1926

Years	1921	1922	1923	1924	1925	1926
Gross harvest in metric tons	3,963	11,383	15,565	6,927	42,105	38,277

Thus it was not possible to provide for the necessary quantity of seed before 1925, but in this year it even became possible to store a certain amount of it. Beginning with 1923, comparative tests were carried out annually for sugar-beet varieties released by Soviet selective breeding stations. These tests included varieties obtained from foreign firms. The very first test made in 1923 proved that in root yield the varieties released by several Soviet stations deserved first place. The varietal tests made in subsequent years often confirmed this, triumphantly announced as a great achievement of Soviet selective breeding work Actually it was a propaganda trick which even its claimants did not believe; within a span of four years, or two generations, how could there have been such progress at a time when the selective breeding stations were only resuming activity and future selective breeding methods were just being outlined? Actually it was the result of the work of selective breeding stations in the pre-revolutionary period, where, by repeated selection, strains of beets had been obtained that were better adapted to local conditions than the imported varieties. As regards sugar percentage, the first place was invariably occupied by the Polish variety Janacz; next came the varieties from stations which had in the past carried on selection aimed at increasing sucrose percentage, for example, the Kalnik station.

APPLICATION OF EXPERIMENTAL WORK TO SELECTIVE BREEDING. In 1920–1923 the Plant Variety and Seed Production Administration reorganized a large number of experimental stations and succeeded in revivifying the Network of Experimental Fields, the continuation of the prerevolutionary organization which had by 1919 fallen into complete decline. The results of experiments carried on by the Network were published. The Network of Experimental Fields was subsequently discontinued as an independent organization, and the separate plots comprising it were assigned to men in charge of the different experiment stations, each of which became the regional center of scientific investigation on sugar-beet cultivation. To coordinate the work of these stations, the Administration called periodic meetings on experimental work (77)[8].

[8] Among those outstanding in scientific work were the following: Nesterov, Solyakov, the Philippovski brothers—Alexander and Alexis—Yakushkin, Dushechkin, Nadezhdin, and others.

STUDY OF PESTS AND DISEASES AND OF THEIR CONTROL. During the first years of work the men at the selective breeding and experiment stations met with an exceptionally large number of pests and diseases of sugar-beets. Special branches for the control of pests and diseases of industrial crops were organized within the stations. The work of entomologists and phytopathologists bore good fruit. At the scientific meetings arranged by the Plant Variety and Seed Production Administration, the entomologists and phytopathologists usually comprised a separate section. Much interest was manifested in the study of the biology of the pests and of the causal agents of plant diseases, in the estimate of harm caused by them, in the study of measures for their control, and in methods for predicting their appearance in mass numbers. The scientific contributions of entomologists and phytopathologists were printed in publications of the Administration as well as in special periodicals.

PUBLICATIONS. The Administration undertook to translate into Russian a considerable number of papers on selective breeding and cultivation of sugar beets (article by Fruwirth, Roemer, Munerati, Zalenski, Zalesski and others). Among the material printed were manuals on biometry; theoretical papers on sugar-beet selection (29, 30, 80, 81); description of soils in beet-growing regions; climatic summaries for beet-growing regions (14); and a series of monographs on pests and diseases. A. Tabentski made up an atlas of drawings on the anatomy and biology of the sugar-beet (73).

In addition to this, the Administration issued periodical and series publications with articles on both scientific and organizational subjects (12, 62). The majority of breeding stations also published their scientific paper.

RESEARCH INSTITUTIONS OF THE SUGAR INDUSTRY

In 1921 the Scientific Institute of Selective Breeding (Nauchnyi Institut Selektsii) was organized to do research work on problems beyond the ordinary practical limits)[9]. Members of this Institute worked mostly in laboratories of the Kiev Agricultural Institute. Papers by members of the Institute were printed in "Trudy Instituta" (Works of the Institute) (78). The Institute

[9] The first scientific director of the Institute was Professor Kolkunov.

continued its activity until 1930, when it was incorporated in the newly-organized All-Union Institute of the Sugar Industry (Vsesoyuznyi Institut Sakharnoi Promyshlennosti).

The center of scientific research on the technology of beet-sugar production was at first a department for the technology of agricultural production at the Kiev Agricultural Institute.[10] A series of reorganizations finally resulted in the founding of the All-Union Institute of the Sugar Industry (Vsesoyuznyi Institut Sakharnoi Promyshlennosti) in Kiev, which was entrusted with the responsibility of scientific leadership of the selective breeding and experiment stations. The All-Union Institute of the Sugar Industry was organized on the basis of three discontinued institutions—the Scientific Institute of Selective Breeding, the Experimental Institute of the Sugar Industry, and the Plant Variety and Seed Production Administration of the Sugar Trust. The new Institute followed three directions: scientific investigations in the fields of genetics and selective breeding of sugar-beets; work on problems in the technology of beet-sugar production; directing the activities of the selective breeding and experiment stations.

The All-Union Institute of the Sugar Industry issued one regular publication (36). In addition to this, collected volumes were published annually in which the results of scientific investigation work were summed up for each completed year (46).

The results of many years of scientific research were permanently recorded in a large three-volume publication entitled "Sveklovodstvo" [Beet production] (72).

There was a certain amount of duplication in the scientific research on sugar-beets in the U.S.S.R. because, in addition to the All-Union Institute of the Sugar Industry in Kiev, there was also the Central Scientific Research Institute of the Sugar Industry (Tsentral'nyi Nauchno-Issledovatel'skii Institut Sakharnoi Promyshlennosti) in Moscow. This Institute concerned itself mostly with problems of technology of beet-sugar production and dealt partly with problems of field work, especially in the so-called new regions of beet growing. The Moscow Institute also had its own publication (79). The sugar industry was supplied with sugar-beet seed by another organization, the Plant Variety and Seed Production Trust (Sortovodno-Semennoi Trest).

[10] The department was later reorganized as the Experimental Institute of the Sugar Industry (Eksperimental'nyi Institut Sakharnoi Promyshlennosti).

DISORGANIZATION BY NKVD AGENCIES, DESTRUCTION BY WAR, AND POSTWAR RECONSTRUCTION

The question naturally arises, as to what the reasons were for the blossoming of selective breeding work in the 1930's. The answer lies in the interest shown by specialists in scientific research and applied research in the realms of biology, genetics, selective breeding and seed production of sugar-beets and in related fields of investigation. Men put their whole souls in this type of work and tried to forget about all the loathsomeness of political squabbles, reports and intrigues. People worked overtime, without additional remuneration, in order to accomplish what they had set out to do. This creative work was constantly interrupted by sudden and unexplained arrests. People disappeared, and it was dangerous to inquire into their fate. Only after a long interval following their arrest were rumors heard about their fate. It appears that these arrests were due to a number of causes, as follows:

a) The pathological suspiciousness of NKVD organizations, not only toward specialists of the old school but also toward the new men, even Party members, as soon as it was noticed that they were devoted to their specialty, taking their work too close to heart and, with their work as common ground, were becoming close friends with other specialists.

b) Denunciations caused by envy, ill-will or the desire to settle personal grudges.

c) A careless word or ironical remark in the company of a group of people, one of which would be a secret agent of the NKVD or an informer who wanted to demonstrate his zeal to his superiors.

Thus along with the creative constructive work carried on with extreme devotion by specialists, destructive work by organs of the GPU and later the NKVD was going on.

In 1937–1938 these arrests assumed a mass character, and by the early part of World War II, a large number of specialists had been done away with. In the present article I do not wish to dwell on the disaster that overtook many Russian geneticists, headed by Academician N. I. Vavilov, because Lysenko made use of the worst methods of political influence and intrigue in his discussion of agricultural problems with these men, and thus

placed his opponents at the mercy of NKVD. I wish to mention only the fate of specialists well known to me who worked in the realm of selective breeding and experimental work in the field of sugar-beets. The following men disappeared, one after the other, in jails and in exile, or died as the result of the cruel treatment in the cellars of NKVD:

B. A. Panshin who had organized the Plant Variety and Seed Production Administration and who for many years directed its activity; B. N. Lebedinsky, selective breeder at the Ivanovka station, later in charge of the selective breeding division of the All-Union Institute of the Sugar Industry; I. I. Voitkevich, selective breeder at the Veselo-Podol' station; V. V. Kolkunov, professor of the Kiev Agricultural Institute and director of the Scientific Institute of Selective Breeding; V. A. Rakoczy, research associate of the All-Union Institute of the Sugar Industry; V. A. Lebov, specialist on seed production; a large number of prominent specialists in research work, such as A. F. Nesterov, P. A. Solyakov, brothers Alexander and Alexis Philippovski, and I. I. Shaposhnikov. It is impossible to enumerate all the victims of terrorism, I have given only the names of those mentioned elsewhere in this paper. As I have already pointed out, among those who died were not only non-Party specialists; one after the other the directors of the Plant Variety and Seed Production Administration and the leaders of the All-Union Institute of the Sugar Industry and of the selective breeding stations were arrested and then vanished.

Thus, even before the outbreak of World War II, NKVD agents wrought havoc among the specialists who worked in the sugar industry, and this disruption was much more severe than that caused by the invading German armies. The war ruined the selective breeding work completely. During the war the seed material, the equipment and the specialists at all the stations located in the European part of the U.S.S.R were evacuated. Selected breeding work at Uladovka and L'gov was transferred to the Biisk station in western Siberia, while all the remaining selective breeding activities (along with the All-Union Institute of the Sugar Industry) were moved to the Kirghiz station in Central Asia.

Before the termination of the war, the equipment, the seed stocks and the selective breeders themselves began to be returned to the

old places. During 1945 and 1946 the destroyed stations were re-established and work was resumed (43, 45).

Development of Selective Breeding Methods

As stated earlier, up to World War I the selective breeding techniques for sugar-beets were developing successfully in the former Polish Kingdom and in the Ukraine. Seeds from foreign firms, such as Vilmorin, Rabbethge und Giesecke, Dippe and Schreiber, were imported for use as original material for selection. As a result of selection, the first parent stock was obtained to serve as original material for further selection at Soviet selective breeding stations.

MASS AND INDIVIDUAL SELECTIVE BREEDING

The development of selective breeding methods in the U.S.S.R. is characterized by a gradual change-over from mass to individual selection. During the first years of operation, selective breeding stations used the mass method of selection because of the lack of beet seed and the need of producing it quickly and in large quantities. Gradually and without completely discarding mass selection as a basic method, workers at some of the stations began to use individual selection. The extent of individual selection practised can be judged by the number of generations (lines) that were grown and studied in comparative test plots. In 1924, the number of these lines at all the selective breeding stations of the Sugar Trust was 2,820, while the total area of the comparative plots was 39 hectares (96 acres); by 1935 the corresponding figures were 10,895 [11] lines and 137 hectares (337.7 acres) (16).

The progenies of the selections were planted out in groups and allowed to cross pollinate. Due to self-sterility which is usual for sugar-beets, the subsequent generations produced by this method may largely consist of individual-family selections. Since it is important to know the male parent which is to furnish the pollen, Soviet selective breeding stations have worked out methods for regulating pollination. Uusally the lines are combined in such a way that pollination occurs within material of a definite origin or type (high tonnage, high sugar or normal). However, since the selected lines themselves represent as yet an unknown quantity in

[11] This figure includes the results of mass and group selection.

regard to their inherent value, the element of accident is not excluded in the process of pollination.

The next step in regulating pollination was to introduce some well-known material as a common pollinator for all the pedigree stock. For this purpose, workers at some of the stations tried to make use either of some well-known populations or, more rarely, of clones that were grown in sufficient amounts and were annually propagated; this was done when the method of diallel crosses was being used. Before World War II, Savitsky had worked out methods for regulating pollination by making diallel crosses (58). This work was interrupted by the war before any practical results could be achieved.

WORK ON INBREEDING

After the studies of Hjalmar Nilsson appeared in print, the attention of some of the Soviet breeders was turned to inbreeding. At first, breeders tried to find self-fertile races (6, 20, 21). Those found were studied from several points of view. The degree of their self-fertility was determined by two methods: *a*) by calculating the per cent of seed balls that had set inside the isolators, or *b*) by the method of Harechko-Savitsky (61), namely, determining the number of ovules fertilized inside the isolators.

Subsequent generations were obtained with the use of the inbreeding method in the two following ways: *a*) by producing seed by selfing with the aid of artificial isolation of self-fertile individuals (21), or *b*) by making related crosses under isolators (4, 6), i.e., by sib-mating as proposed by Munerati. The first generation from inbreeding showed considerable variation in shape of the leaf rosette, but from the third generation on, there was a gradual increase in morphological uniformity within the limits of each line; in the fourth and fifth generations the lines became practically uniform. Among deformities and anomalies in the inbred progeny (6, 21) may be listed the appearance of dwarf plants, of forms with short petioles or with petioles grown together, with reduced thread-like laminae, together with non-viability of seeds. Among new characters that appeared in the splitting of certain inbred lines, Grinko (21) recorded cleistogamy, monogerm seed and resistance to *Cercospora*.

Archimowitsch found one form that had unisexual female

flowers (6), and Kolomietz located a form with unisexual male flowers. Later these forms were studied in detail by Finn (17). The study of the effect of inbreeding on root weight and sugar per cent was continued to the sixth generation (21). In regard to yield, the low-tonnage lines predominated. Only very rarely did lines split off, whose tonnage exceeded that of the original variety. Usually even the very best inbred lines showed depression in subsequent generations.

The very opposite was observed in regard to sucrose percentage (21). From the inbred lines both high and low-sugar types were segregated. Use of selective breeding for the purpose of increasing quality led to positive results. Studies of the results of hybridization between inbred lines for the purpose of finding successful combinations that manifested heterosis were initiated later, when a sufficient number of older generations of inbred lines had accumulated.

At the Verkhnyachka selective breeding station, one mating of inbreds distinctly manifested heterosis for two successive years (1932 and 1933).

At the Ivanovka station, positive effects of heterosis were observed from mutual crosses among a large number of lines (21). However, these lines were not increased, and subsequently, after Lysenko's attack against inbreeding, even the most zealous followers of this method relinquished this dangerous path of research.

METHODS AIMED AT ELIMINATING UNDESIRABLE EFFECTS OF RELATED CROSSES

As stated by Savitsky (58), beginning with the second generation of individual selection in sugar-beets, a cross between plants that are related in origin takes place and as a result there is a decrease in yield. To prevent this undesirable phenomenon, Savitsky proposed to make an evaluation of the yield of the parents (pedigree) with the aid of diallel crosses. In order to do this the pedigree stock should first be propagated vegetatively. For use as pollinators, clones that had been thoroughly studied and sufficiently propagated were to be taken.

In addition to this plan, Savitsky proposed a number of others designed to prevent the undesirable consequences of close breeding. Crosses were suggested between populations, between the progenies of individual selection, inbred lines, etc. (55, 56).

These methods were being tried out at some of the stations when the war stopped their progress.

MORPHOLOGICAL SELECTIVE BREEDING

The morphological method of selective breeding for sugar-beets was used in Russia long before World War I but came into full bloom during the early period of Soviet selective breeding. In some instances, direct selection methods were used (for example, for size and shape of root) with fairly good success. But in most cases selection was done by indirect methods. Correlations were found between size and shape of root and its sugar content, between morphological characters of the leaf rosette and the root characters (weight and per cent of sugar). Very extensive calculations were made in order to find coefficients of correlation between these characters. By no means all of the scientists had a favorable opinion of the morphological method of selective breeding in the way it was practised at the selective breeding stations of the U.S.S.R.

Savitsky (54) pointed out the pitfalls involved in using correlations, and he recommended that close attention be given to the degree of variability of characters; Votchal has often stated that the use of crude methods of quantitative estimates for degree of character expression, as used by selective breeders under field conditions and without taking into account the ecological influence of environment, can not give positive results. Indirect selection by morphological characters has not realized the hopes that were placed in it in the U.S.S.R. The outcome of this temporary enthusiasm was the appearance in print of classifications of morphological types of beets by characters of the leaf, leaf rosette and the seedling.

These methods of classification of separate organs of the beet plant were well suited either for quick selection or for brief descriptions.

A résumé of the results of morphological studies of the beet plant is given in a paper by Archimowitsch (7).

In the paper by Savitsky, results are given for his studies of the degree of variability and correlation between a large number of morphological and utilitarian characters of the beet plant (51, 52, 53, 54).

An example of success with the use of direct morphological

selection is the production of a monogerm race of sugar-beets. This work was successfully carried out at the All-Union Institute of the Sugar Industry, under the leadership of Savitsky who continued and successfully completed this work in the United States.

SELECTIVE BREEDING BY ANATOMICAL (HISTOLOGICAL) CHARACTERS

Selective breeding of sugar-beets by their anatomical characters was proposed in 1907 by Professor V. Kolkunov (24). In checking over old data by Schindler on the correlation between the size of parenchyma cells in the root and its sugar content, he discovered a connection between size of parenchyma cells of the root and of the leaf, and on this basis proposed his own method of selection by the anatomical characters of the leaf.

At the same time, Kolkunov found the existence of a difference in the intensity of transpiration in different races of the same plant species (sugar beet, wheat), races that differed from each other in the size of their cells. On this assumption he proposed the theory of drought resistance of plants, given in more detail in one of the subsequent contributions (25). This theory was not accepted; a criticism of it is given in one of the papers by Maksimov (33).

Selective breeding by anatomical characters did not yield any practical results, but it helped to arouse interest in the U.S.S.R. for making anatomical studies of the beet plant. A. Tabentski made up an atlas on the anatomy of the sugar-beet, in which he collected a large number of drawings that had been scattered over various publications printed mostly abroad and, for this reason, not easily accessible to Soviet selective breeders (73). In addition, he and his associates contributed a number of original papers on the study of the details of anatomical structure of the beet plant (74).

SELECTIVE BREEDING ON THE BASIS OF VIGOR DURING INITIAL GROWTH OF SEEDLINGS

The old records by H. Briem (1900) on the relation between the weight of seeds from the same seedball and the size of seedlings and, eventually, the weight of the adult plants, attracted the attention of many investigators who tried, in one way or another, to confirm these findings and to use them for purposes of selective

breeding. Special mention is deserved by Zadler (82) who made some careful studies on this subject.

During the prerevolutionary period, observations on growth rate in sugar-beets were made by Dushechkin, Nikolski and A. Philippovski. The last-named returned to these studies some time later and established the fact that high-tonnage varieties differ from high-sugar varieties by the greater weight of their seedlings during early development stages. Savitsky pointed out the variation in degree of correlation between weight of leaves and weight of roots. The coefficient of correlation between these two is more striking during the first development stages and decreases toward the end of the vegetative season. On this basis the author pointed out the advantages of selecting plants that appear outstanding in vigor during the early stages of growth. This postulate was checked in 1936, and subsequent tests on the progeny affirmed the correctness of this theory (57).

Mazlumov at the Ramon selective breeding station used vigor of growth during the initial phases of development as the basis for selection. For this purpose, from 2,000 to 4,000 of the best plants are annually singled out in the selective breeding fields and observations are periodically made on these plants. Final selection is made after laboratory analysis (34, 35)[12].

Goodwill at the L'gov breeding station has evaluated the progeny on the basis of rate of growth during the earliest developmental stages under laboratory conditions. He believes it possible to discard on this basis the less desirable individuals of the progeny (from 30 to 35 per cent) and in this way to reduce considerably the size of the test plots (23)[13].

SELECTIVE BREEDING FOR EARLY MATURITY AND DROUGHT RESISTANCE

Selective breeding for early maturity is of great importance, not only for the northern beet planting regions with a short vegetative season (the regions of Kursk and Voronezh in the European U.S.S.R., western Siberia in Asia) but also for other regions. The fact of the matter is that the harvesting of beets in the

[12] One of the more valuable varieties of the Ramon station (28-06) was introduced as a result of this method (35).

[13] However, this hypothesis was not proven scientifically, and other stations do not use the method.

U.S.S.R. is very prolonged and there is often the danger that a part of the harvest may perish in the field in winter. It is therefore recommended that the harvesting begin very early (September 5 to 10); this requires early-maturing varieties.

Progress in this direction has been made at the Ramon selective breeding station, and varieties produced on this station have always taken first place in comparative tests at the Biisk selective breeding station which is located in a region with a very short vegetative season.

Selective breeding for drought resistance is of great significance for the southern beet-growing regions. For this reason a great number of investigators, Kolkunov, Votchal and Orlovsky among others, gave special consideration to working out a method of selective breeding for this character (42).

No reliable and practical method was found, but prolonged selective breeding under definite ecological conditions left its mark on the properties of some of the varieties. Thus, for example, sugar-beet varieties produced at the Kharkov selective breeding station under insufficient moisture were outstanding in tonnage when grown under these conditions; on the other hand, varieties from the Uladovka station, produced under conditions of sufficient moisture, are outstanding in tonnage when grown under more humid conditions (42).

SELECTIVE BREEDING FOR RESISTANCE TO FUNGUS DISEASES

Among the most widely spread fungus diseases of sugar-beets in the U.S.S.R., the following should be listed: the so-called root rot (Wurzelbrand of German authors) caused by the fungus *Phoma betae* Frank; leaf spot caused by *Cercospora beticola* Sacc.; and storage rot produced by the fungus *Botrytis cinerea* Pers.

The curly top disease which is widespread in the United States is not found in the U.S.S.R. Some progress has been made in the control of storage rot. Since it is necessary to store roots in bins over the prolonged winter period, this disease is of special importance to the U.S.S.R. V. Shevchenko, pathologist at the Byelaya Tserkov selective breeding station, worked out a method for determining the resistance of individual roots to this infection (65). This method adds another character to the list to be considered in selective breeding of new varieties.

TECHNIQUE OF FIELD WORK

In choosing an area to be used for selective breeding or as control plots at the selective breeding stations, the demands regarding contour and uniformity of soil fertility are usually rather strict. All cultivation and fertilizing of the soil is carried out as uniformly as possible and is completed in the shortest possible time. The control plots are planted either by hand in clusters or by machine in rows, depending on the amount of available seed or on the size of the plot. The planting is usually done in six or in eight repetitions.

LABORATORY TECHNIQUE

The laboratories in which sugar determinations are made at the selective breeding stations of the U.S.S.R have undergone considerable change. Originally the laboratories were equipped with manual apparatus for taking root samples in the form of pulp for testing (Herles knives and Volsky presses). Before World War II most of the stations were equipped with Keil-Dolle mechanical tools. For making determinations of sugar per cent, the stations used the method of cold digestion after Sachs Le Docte.

Some of the selective breeding stations worked toward decreasing the amount of harmful nitrogen and other constituents of molasses (Ramon, Veselo-Podol, Pervomaiskaya); they also made determinations of the purity of the juice. The per cent of dry matter in the juice was determined with the aid of a refractometer. Determinations of harmful nitrogen were made by the colorimeter method of Friedl.

VEGETATIVE PROPAGATION OF THE BREEDING MATERIAL

To increase the amount of seed obtained from one root, the workers at Soviet selective breeding stations either cut the roots lengthwise into several sectors or used vegetative propagation after the method of Nowoczek (1890). If the cutting of the roots is carefully done and if the sectors obtained are planted, it is possible to double or treble the yield of seed from single roots; sometimes it is possible to increase the yield five or six times so that over one kilogram of seed can be obtained from one root.

With Nowoczek's method the yield of seed is considerably greater than with the first method, and with the use of repeated

vegetative propagation, the chances of increasing the quantity of seed from one clone are unlimited. As already stated, the possibilities of unlimited increase in the number of individuals from one clone enabled breeders to use well-known clones as general pollinators for producing elite stock.

CONTROL OF POLLINATION

Regulation of pollination in the work of Soviet selective breeding stations was studied from two angles: the theoretical angle, which consists of ways of finding desirable pollinators as previously discussed; and the practical angle, which aimed at working out techniques that would guarantee self-pollination or would assure a cross in the desired direction.

The various techniques for regulating pollination in sugar-beet can be summed up as follows:

ISOLATION

a) Artificial isolation of individual plants or their parts for the purpose of obtaining seed from selfing.

b) Artificial isolation of paired individuals for the purpose of obtaining hybrids either closely or distantly related.

c) Isolation of small groups of plants, artificially or by distance, for the purpose of increasing the breeding stock.

d) Distance isolation of large plots of seed beets for propagation of varieties.

HYBRIDIZATION

a) Matings made under isolators after preliminary emasculation of flowers followed by dusting of pollen.

b) Matings made under isolators without emasculation and without artificial pollination.

c) Matings of predetermined combinations of varieties under free-blooming conditions of the parents and with the use of distance isolation for each combination.

Investigations were started by the author of the present paper in 1923 along the lines outlined above. In addition to these investigations, the author considered the following problems:

a) A comparison of types of artificial isolators advocated by other investigators: H. Nilsson, Munerati, Levallois, Frederiksen; their improvement and the design of new types (3, 8).

b) Determination of the distance practical for use in distance isolation (4).

c) A study of the role played by insects in the pollination of beets, begun by the author in the Ukraine (2) and continued in Spain (10, 11).

Among papers by other workers on the subject of methods for regulating pollination, the following should be mentioned: the work by Harechko-Savitskaya on making artificial crosses (59) and the studies by Fyodorovich (15) and Herman (19) on the distribution of pollen in the horizontal and vertical directions.

There is no need to discuss in detail the results of investigations for regulating pollination because they have been sufficiently described by the author in other summaries (5, 9).

SPEEDING UP THE PRODUCTION OF A GENERATION

To speed up the production of a new generation, two methods are used in the U.S.S.R.:

a) At selective breeding stations that have no greenhouses, seed that has been harvested the same year is planted in the field at the end of the summer. Under conditions prevalent in the Ukraine, the plants have 70 to 80 days for development before the termination of the growing season. The average weight of the root at harvest time, late in autumn, may be as high as 60 grams, sometimes as high as 125 grams. Every generation of this type is subsequently planted out in a group and separated by distance isolation from the others; in this manner a sufficient quantity of seed for making further tests of the progenies becomes available at once.

It must be noted, however, that this method, which has been given the name of "fall planting," can not be regarded merely as a technical method used for propagation of material because the quality of F_2 obtained under conditions of related propagation will differ substantially from the quality of F_1 produced very often by pollination with varied material.

b) The All-Union Institute of the Sugar Industry and the selective breeding stations that are equipped with greenhouses or hothouses obtain seed in wintertime from especially valuable stock. To force plants to bloom and produce fruit in winter in a greenhouse, it is necessary to grow them first under low temperature

conditions (+ 8 to + 10° C.) for a period of one and one-half to two months and under constant artificial illumination (49).

Sugar-Beet Genetics in the U.S.S.R.

Sugar-beet genetics in the U.S.S.R. has been concerned with variability of characters in the plants, the inheritance of morphological and quantitative characters (weight of root and per cent of sugar), the cytology of the genus *Beta* and chromosome aberrations in sugar-beets, and with a number of other problems. The study of modificational variability was started by V. Savitsky at the Byelaya Tserkov selective breeding station and was continued by him in Kiev at the All-Union Institute of the Sugar Industry. To obtain genetically uniform material, Savitsky used vegetative propagation of the material to be studied. Simultaneously, variability was also studied within populations. The degree of variability of the characters was determined by the size of the coefficient of variability (51–54). In this manner slight or strong variability of characters was determined. This gave a number of valuable pointers for practical selective breeding and served as a preliminary index for genetical analysis of the best plant.

For genetical analysis, Savitsky made a number of hybridizations, both intra- and interspecific. The products from this work were utilized in increasing original stocks for practical selective breeding.

Intraspecific crosses were obtained between sugar, semi-sugar, fodder, table beets and mangold varieties; also between cultivated and wild forms of the species *Beta vulgaris* L. Analysis of the progeny of the crosses permitted the establishment of several laws of inheritance with respect to root weight and sugar per cent (58).

Crosses between the root types (sugar, semi-sugar, fodder, table beet) and leaf types (mangolds) proved to be of great interest. Especially successful were combinations involving the green forms of mangold. The sugar content in F_1 crosses of sugar-beets with mangolds was usually higher than the average for both parents, and in the older generations there appeared hybrid lines that were higher in sugar than the original forms of the sugar-beet. Hybrids of the sugar-beet and the North European forms of wild beet also attracted attention as possible material for further increase in sugar content (58). Hybrids between

sugar, semi-sugar, fodder and table beet were also tested. F_1 hybrids between sugar-beet and other root forms of beet disclosed an intermediate type of inheritance in regard to sugar per cent.

With the use of saturating crosses accompanied by selective breeding, Savitsky (58) succeeded in producing, in the older hybrid generations, forms that combined the sugar content of the sugar type with high tonnage. Before the outbreak of the World War II, a number of strains produced by Savitsky from hybrid material were turned over to selective breeding stations for tests. They passed the tests successfully and after the war were propagated for commercial use (45).

Hybrids between sugar-beet and wild *Beta vulgaris* proved to be very promising, just as they were in the work of many western European scientists, for purposes of producing lines resistant to *Cercospora* (87). Among the hybrids between fodder or table beet and the green forms of mangold or the North European races of sub-species *maritima*, Savitsky found forms that were phenotypically similar to the sugar-beet. Interspecific crosses were made at the All-Union Institute of the Sugar Industry in Kiev by V. Zosimovich. For the purpose of collecting seed of the wild species of the genus *Beta*, Zosimovich had made two expeditions to Crimea and to the Caucasus. After a critical study of species belonging to the genus *Beta*, Zosimovich proposed his own system of classification for this genus (88). Following the method of Transhel (75), he divided it into three sections—Corollinae, Vulgares, Patellares—and reduced the number of species in this genus to ten. He separated a new species, *Beta corolliflora* Zoss, under which he grouped forms with 36 chromosomes ($2n$) which have a phenotypic resemblance to *Beta trigyna* W. et K. In the latter species he retained only forms with 54 chromosomes ($2n$). Zosimovich considers this species a natural amphidiploid from a cross between *B. lomatogona* F. and M. and *B. corolliflora* Zoss. By making the most varied crosses, Zosimovich (86) obtained the following hybrids:

B. vulgaris L. ($n=9$) $\times$ *B. corolliflora* Zoss ($n=18$)
B. vulgaris L. ($n=9$) $\times$ *B. lomatogona* F. et M. ($n=9$)
B. vulgaris L. ($n=9$) $\times$ *B. macrorrhiza* Stev. ($n=9$)
B. corolliflora Zoss. ($n=18$) $\times$ *B. lomatogona* F. et M. ($n=9$)
B. corolliflora Zoss. ($n=18$) $\times$ *B. macrorrhiza* Stev. ($n=9$)

B. lomatogona F. et M. ($n=9$) × *B. macrorrhiza* Stev. ($n=9$)
B. lomatogona F. et M. ($n=9$) × *B. trigyna* W. et K. ($n=27$)

The cytology of the genus *Beta* was also studied in detail. In numerous papers (e.g., 28, 66) data by Winge (1917) and Artschwager (1927) on the number of chromosomes in *Beta vulgaris* L. were confirmed ($n=9$). The number of chromosomes in other species of *Beta* was also investigated. These included *B. trigyna* W. et K., *B. patellaris* Mogs., *B. macrorrhiza* Stev., *B. patula* Alt., *B. lomatogona* F. et M. (67, 68). H. Savitsky and V. Savitsky found poly- and heteroploid forms (61), and two heteroploid forms of sugar-beet with 26 and 28 chromosomes were detected. The progenies from crosses of these forms with each other and with ordinary diploid races contained polyploids ($3n$, $4n$, $5n$) and heteroploids ($2n+1$, $2n+2$, $2n+3$, $3n+1$, $3n-1$). Cytological chimeras were studied in great detail (61). Attempts were also made to obtain polyploid forms experimentally by the method of Jorgensen (27). However, further studies of forms obtained by this method disclosed the fact that they are cytological chimeras (61).

Chromosome morphology was first studied by N. Kuzmina (28) and later at the cytological laboratory of the All-Union Institute of the Sugar Industry under the supervision of Helen Savitsky.

Morphological studies of chromosomes of the species *B. vulgaris* L. were made by N. Zaikovskaya (84) and M. Sirotina (66).

A morphological description of chromosomes of other species of *Beta* was furnished by Sirotina (67, 68). A summary of studies on the cytology of the genus *Beta* is given by Savitsky (61).

Sugar-beet embryology attracted the attention of many investigators on various topics—reduction division (32, 61); pollen grains and embryo sac (13, 39-41, 61); and double fertilization (61). Further development of the embryo was described in papers by P. Oksiyuk, B. Favorski and H. Savitsky.

H. Savitsky was the author of a detailed summary on the embryology of sugar-beet (61). Much attention was given to the cause of self-sterility. As H. Savitsky has demonstrated in her investigations, the reason for this phenomenon in most races of sugar-beet is to be found in the slow growth of pollen tubes where self-pollination occurs (61). In the course of breeding work self-

fertile races were found at many of the selective breeding stations (6, 20). A study of these races resulted in the discovery that the character of self-fertility is dominant (6, 21). An embryological study of self-fertile races was made by N. Zaikovskaya (83), following the method outlined by H. Savitsky (61). It was noted that the self-fertile races differed from each other in the rate of growth of the pollen tube. This method enabled Savitsky to make a more detailed study of the biology of propagation in sugar-beet populations (61). Savitsky grew self-sterile clones during their blooming season in chambers kept at a temperature from + 10 to + 12° C, and obtained seed by selfing, thus proving that the character of self-fertility depends for its expression on the surrounding temperature at time of flowering (60).

Commercial Sugar-Beet Varieties

METHODS OF PREPARING COMMERCIAL VARIETIES

Up to 1925 the basic method of preparing commercial varieties at Soviet selective breeding stations was by the propagation of roots which had been obtained by mass selection. After 1925 this method was discarded and replaced by a new one which was used until 1930. This consisted of propagating, without selection, the best numbers of the elite varieties from selective breeding stations that had been given a good rating in comparative tests. This method involved propagation within the limits of related lines, and, as a result, there was a lowering of the commercial qualities of the variety produced (regression).

For this reason the method was changed from 1930 on. In preparing a commercial variety thereafter several elite lines were mixed in such a way that mutual pollination would occur when the plants were set out in the field. This method undoubtedly had a number of advantages over the previous one because, in the first place, it reduced the length of time required for related propagation; in the second place, due to mutual pollination of elite lines, the drop in yield caused by pollination between closely related lines can be avoided. Finally, this method gives the breeder the opportunity to study combinations which manifested heterosis and, in his further work, to produce such combinations as required. The literature on the subject up to that time contains no references showing that such combinations had been found.

EVALUATION OF SUGAR-BEET VARIETIES

In one way or another the newly formed varieties are given a final rating in the governmental comparative tests. The method of arranging these tests, the statistical work on the data and the results of experiments have been described in detail in the publications of Solyakov (69, 70) who was for a long time in charge of the test plots of the Plant Variety and Seed Production Administration of the Sugar Trust.

From 1923 to 1930 the method of utilizing data from governmental comparative tests consisted of evaluating each variety on the basis of all of the points considered in the test. Only the highest-scoring varieties were propagated and released to factories. The remaining numbers were discarded. Many varieties that had been discarded on this basis were very productive in certain regions and very frequently in areas where such varieties originated. This method did not take such factors into consideration. Rakoczy (50) was first to point out this fact. From 1933 on, the release of mother beet seed for reproduction (production of commercial seed) was based on regional properties of the varieties in accordance with the results of tests carried on in different localities (26).

In this manner, seeds that had been obtained as the result of many years of selective breeding work, and after proper evaluation, are released to factories; thus a given lot of seed (or variety of seed, according to Soviet terminology) ceases to exist. Recently attention has been called to the disadvantages of this system. After a Congress on Sugar-beet Selective Breeding in 1939, the best varieties were employed several years in succession, using repeated reproduction together with selection for improvement of quality (44).

VARIETIES OF SUGAR-BEETS

Under the term "varieties", Soviet selective breeders understand all elite lines or a mixture of such lines of given properties, which are propagated for commercial purposes (26).

It would be more correct to understand by this term the elite stock or line numbers created and kept in production at a selective breeding station by means of constantly repeated selection, aimed in a certain direction, which form the seed lots released by the selective breeding station for planting.

The desired properties of varieties released by Soviet selective breeding stations have been frequently changed. During the early period the stations placed emphasis chiefly on high-sugar types. This was the result of the selective breeding work of the preceding era. Among the stations that produced high-sugar varieties were Verkhnyachka, Nemercha, Kal'nik and Udychsk; the last two were subsequently closed. Later it became evident that the emphasis on high-sugar types was unprofitable; however, the breeding material of the high-sugar types was not destroyed but gotten together and stored at stations Veselo-Podol' and Yaltushkovsk.

From 1923–24 on, i.e., from the time when data on the first comparative tests made by the Soviet government were published, high-tonnage types have been preferred. These types naturally attracted attention at a time when there was a lack of raw material for the sugar industry. The high-tonnage varieties were and still are released by the following stations: Uladovka, Ivanovka, Byelaya-Tserkov, L'gov, Ramon, Biisk, Kirghiz.

Beginning with 1934, attention was directed to the normal type of beet that combined sufficiently high sugar content with high tonnage. Especially outstanding in this respect were varieties from the Verkhnyachka station. Stations Uladovka, L'gov and Ramon have partially changed over to developing this type.

PROPAGATION OF HIGH-QUALITY VARIETIES

Seeds of outstandingly good rating at governmental comparative tests are designated in Soviet terminology as " mother beet seeds ". They are planted out to obtain mother beets [14]. Late in the fall, the mother beet roots are harvested and stored in bins until next spring when they are planted out in the field again to produce seed. These, designated as factory seed, are released to factories.

Of great importance in growing mother beets is the production of the greatest possible number of roots (stecklings) per hectare. This reduces the costs in producing seed. This simple truth was not immediately assimilated by the leaders of the Soviet Sugar Trust, so that, in 1923 for example, each hectare planted yielded enough roots to plant only two hectares for seed. In the course of the next few years this ratio had improved, as shown in Table III.

[14] In contrast to Soviet terminology, these would probably be called stecklings in the United States.

TABLE III. NUMBER OF HECTARES PLANTED FROM ONE HECTARE OF STECKLINGS

Years:	1923	1924	1925	1926	1927	1928
Hectares	2.0	2.6	3.8	4.4	4.1	5.3

Certain changes in agronomic techniques used for mother beets as compared with those followed in growing ordinary beets for sugar production were gradually worked out. These changes can be summed up as follows:

The mother beets are planted somewhat later than the commercial beets, usually in the middle or after completion of planting the commercial beets. The best quantity of seed to plant per hectare is 22–24 kilograms; however, this quantity is sometimes lowered to 16 kilograms per hectare, depending on the quantity of available seed. The spaces between rows in this case are narrower than in growing factory beets, 35.5 cm. Thinning is done in such a way that the beets are more closely spaced than are commercial beets, namely 9.0 cm. With this spacing the theoretical number of roots produced on one hectare should be sufficient to plant 14 hectares of seed beets. Actually this never happens, and the ratio 1 : 5 is considered good.

Harvesting of mother beets is done somewhat later than that of factory beets; it coincides with the advent of cold weather. Beet roots harvested during cold weather store better.

In the northern beet-growing regions (Voronezh, Kursk, Chernigov), cold weather begins in the early part of October, while in the southern parts of the districts of Kiev and Vinnitsa, cold weather begins the third week of October.

During harvest all diseased and small roots—those weighing less than 50 grams—are discarded. Until recently the best size for a steckling was considered 200–300 grams (64). The roots are cleaned of leaves in such a way that the buds on the crown are not injured.

Of great importance is the winter storage of roots in underground bins (trenches). Severe winters do not permit use of bins above ground, as is the practice in western Europe. Packing for storage is done in such a way as to protect the roots from temperatures below 0° C. as well as from temperatures (above + 7° C.) A certain amount of practical experience is needed here because if it is lacking the result may be failure—freezing or decaying of

roots in the bins. During winter storage the temperature inside the bins is watched with the aid of special bin thermometers. If the temperature within the bins varies within the limits of $+2°$ and $+4°$ C. it is considered safe. If the temperature rises or drops, suitable measures are taken.

Until the outbreak of World War II this was the method of growing mother beet roots to be used for planting the following year for seed production.

Before and especially after World War II the ideas of Lysenko were expressed in attacks on the agronomic practice involving the use of mother beets, which had been generally accepted by Soviet seed growers. The attacks consisted mostly of criticism of the old system, since, according to it, each plant was restricted to a small feeding area (35×9 cm.) which limited its development; according to Lysenko's claim, which became fashionable in the U.S.S.R. at that time, good growing conditions could improve not only the plant itself but also its progeny (see 1).

As a consequence, the agronomic practices used in growing mother beets changed after the war as follows: spacing between rows in non-irrigated regions became 35.5 to 44.5 cm.; in irrigated regions, 44.5 to 50 cm.; and the distance between individuals in the row became 15 to 18 cm. the first case, 10 to 12 cm. in the second case. In accordance with instructions for thinning, the most vigorous plants are now left standing, while diseased plants and bolters are removed [15]; small roots are discarded at harvest time. The goal of the grower is to harvest from one hectare of non-irrigated land, 110–120 thousand roots varying in weight from 400 to 500 grams; for irrigated regions the same quantity of roots ranges in weight from 500 to 600 grams. It is considered satisfactory to harvest from one hectare enough mother beets to plant three to four hectares of seed beets.

In spring the roots are removed from the storage bins, are examined in order to remove all diseased and decayed individuals, and are then planted out in fields previously prepared.

The agronomic techniques used in growing beet plants for commercial seed production were worked out gradually. A great deal of experimental work on the technique of growing

[15] Bolters are plants that bloom the first year.

seed beets was done before World War I in the Network of Experimental Fields of the All-Russian Society of Sugar Factory Owners (*37*, 38). During the post-revolutionary period, a great many experiments on their cultivation were carried out at the Ivanovka selective breeding station. Gorodetsky (18) gives summaries of results of experiments carried out mostly by the Network of Experimental Fields and by other experimental institutions until 1924. Later summaries (1, *22*, 63, 64) give the results of subsequent studies.

Thus the techniques for producing commercial beet seeds in the U.S.S.R. can be divided into two distinct operations carried out during two complete vegetative seasons: *a*) spring planting of seed from related mother roots and harvesting of beets at the end of the first vegetative season; *b*) spring planting of roots stared in bins over the previous winter.

The mild middle-Asiatic winters suggested the possibility of planting beet seed in these areas early in August and of allowing the young plants to winter in the field in order to produce seed the following summer. Thus a new method which was given the name of non-transplanting method was started in the U.S.S.R. (1). A comparison of producing by this method with the ordinary method which involves transplanting was carried out for seven years (1941–1947) at the Frunzovskaya selective breeding station with the following results: for five years (1941–1943, 1946–1947) results favored the new method; for one year (1944) the yield obtained by the old transplanting method was higher by an insignificant margin than the yield obtained with the new method; in one year (1945) all the plants were winter-killed.

The authors of the "new" method failed to point out that this method has long been in use in Utah, New Mexico and Oregon.

The seeds produced on seed-producing collective farms are sent to large seed houses (Vinnitski, Lebedinski and Bakhmachski) where they are cleaned, formed into large batches according to commercial categories, then shipped for storage to warehouses. From these warehouses the seeds are delivered to sugar factories and then distributed for planting.

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PROSPECTS OF APPLICATION OF BIOLOGICAL CONTROL IN FOREST PATHOLOGY

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INTRODUCTION

The discovery of penicillin inspired biologists to search for compounds either more active or more specific against human pathogens. Since then many laboratories for the study of antibiotics have been established or expanded, and a number of new antibiotic compounds have been found—all of which has represented progress in the natural sciences. In addition to their human utility, the possible value of these compounds in combatting plant pathogens has been demonstrated (1, 10), and a completely new and extensive field in contemporary applied biology has thus become evident. In the realm of forestry, one section of this field, very limited experiments have shown the possibility of applying the antagonism which exists between certain micro-organisms to the control of forest-tree diseases. It is the purpose of this brief paper to review the literature published so far on the subject and to assess the prospects for effective application.

LITERATURE

The first observation on the antagonism of microflora toward fungi interesting to forest pathologists was that of Harder in 1911 (13) to the effect that *Penicillium glaucum*, a well-known green mold, retards the growth of *Coniophora cerebella*, a common xylophage saprophyte, and that spores of *Stereum purpureum*, a cause of wood deterioration and the first fungus to attack beech logs after felling in some European countries, germinate slowly on a substratum containing metabolic products of this mold. Subsequent publications have been concerned with *a*) the effect of some species of *Aspergillus* on the wood-decay fungi *Merulius lacrymans*, *M. pinastri*, *Ganoderma lucidum* and *Lenzites viallis* (29); *b*) control of a virulent strain of *Fusarium*, causing damping-off of seedlings of *Pinus sylvestris*, by bacteria (*Achromobacteria*, *Pseudomonas* (16); *c*) antagonism of *Bacillus subtilis* and *Phyto-*

monas bacterium toward *Ceratostomella*, the Dutch elm disease fungus (24); *d*) the possibility of controlling rot and blue stain in wet mechanical pulp by an isolated bacterium (*Bacterium* A) (25); *e*) prevention of pine root decay, caused by *Fomes annosus*, by *Trichoderma viride*, *Peniophora gigantea*, *Hypholoma fasciculare* and *Penicillium* sp. (27); *f*) the effectiveness of some soil organisms (*Aspergillus*, *Penicillium*) against *Polyporus* (*Fomes*) *annosus*, a root and heartrot fungus of pines and Norway spruce (26); *g*) the effective antagonism of *Penicillium camerunense* against *Coriolus* (*Polyporus*) *versicolor*, a white decay fungus in many woods (15); *h*) an inhibitory effect in culture of an actinomycete toward *Endothia parasitica*, the chestnut blight fungus (8); and *i*) a parasitic action of *Verticillium* sp. on the aeciospores of *Cronartium asclepiadeum*, the pine blister rust fungus (5).

In England experiments have been conducted to control the spread of *Fomes annosus* by inoculating pine stumps with *Peniophora gigantea*, an antagonist to the other fungus (31); and Rishbeth (28) completed his studies on the antagonism of *Trichoderma viride* against *Fomes annosus* by evaluating the soil properties making possible the growth of the former. Other work has reported *a*) that *Trichoderma viride* successfully combatted *Armillaria mellea* (3); *b*) an efficient inhibitory effect of *Trichoderma viride* against wood-destroying fungi in southern pines treated with fluoride solutions (21); *c*) retardation of *Lenzites* (*Daedalea*) *quercina* and *Coriolus versicolor* inoculated into beech and oak wood blocks soaked in liquid cultures of an undetermined bacillus (17); *d*) that certain conditions contributed to the production of gliotoxin by *Trichoderma viride* in unsterilized soil (30); *e*) that *Alternaria solani* was antagonistic toward *Endothia parasitica* in culture and that the culture filtrates were active against *Armillaria mellea* also (9); *f*) that *Bacillus subtilis* and *Penicillium* were inhibitory toward *Endothia parasitica* in cultures (18); and *g*) that a strain of *Penicillium crustaceum* on beechwood blocks later inoculated with *Schizophyllum commune*, a wood destroyer, had a pronounced inhibitory effect (19). In addition, an explanation (22) has been given regarding the action of *Trichoderma viride*, and a demonstration has been provided (2) of a pH reaction and of the antagonism of this same fungus against *Armillaria mellea* and *Polyporus schweinitzii*.

COMMENTS

From the foregoing very condensed survey of the literature on the subject, it is apparent that experiments concerning biological control of forest-tree diseases have been conducted in various directions. All efforts have been and still are of a purely experimental nature; actual application of biological control to standing trees or to lumber has not yet been reported. The slowness in obtaining more definite information results from the very complex correlations among micro-organisms in their co-existence, from a certain natural balance between them in the locality, and from a number of other known and unknown factors. Successful application of biological control would mean, in certain cases, changing this natural balance by deliberately placing the antagonist organism in the environment of the pathogen but without in this way changing the antagonist's potential.

Amateurs in the biological control of tree parasites claim, in theory, two main advantages in this method of control: *a*) that micro-organisms, since they are endowed with abundant growth and reproduction, are capable of extending their antagonistic action without assistance; *b*) that application would usually be inexpensive. But there are many questions which the limited information provided by experiments so far do not answer, especially regarding resistance of plants under changed environmental conditions, introduction of new parasitic and saprophytic organisms as a consequence of such changes, stability of introduced antagonists and their influence on the soil. Let us further analyze possible conditions attending application of antagonists to parts of a tree, to cut wood and to soil.

The diseases that occur and spread in the soil, like root rot and damping off, have attracted the attention of most experimenters. From the results obtained to this day, it is apparent that a natural unsterilized soil has an effect on antagonists different from that exerted by a sterilized soil. If infected soils do not contain a specific antagonist organism, one way of initiating development of the latter would be by artificial inoculation. In such events different situations may result: *a*) the introduced organism (antagonist) may be prevented from growing or from reproducing by rival organisms or by the chemical and physical constitution of the soil; *b*) the antagonist may develop but be unable to produce any active antibiotic substance; *c*) the antagonist may produce the

antibiotic substance, but other organisms or the chemical composition of the soil may neutralize the latter; or *d*) under the most favorable of circumstances, the antagonist may produce an active and stable substance.

Furthermore, the value of inoculating soil with a desired organism has not yet actually been demonstrated. Brian (4), studying this question, pointed out an inhibitory action of one organism on another in the soil, and other investigators *a*) have noted a suppressive effect of *Aspergillus clavatus* and *Streptomyces griseus* against *Bacillus subtilis*, the producer of several antibiotic compounds (11); *b*) have reported on the ineffectiveness of *Trichoderma viride* toward *Phytophthora cinnamomi* in a simply inoculated soil (6); *c*) have shown that *Penicillium patulum* and *Bacillus* B-6 produce more antibiotic in unsterilzed soil enriched by certain nutrients (12); *d*) have recorded a higher percentage of survival among pine seedlings in soil containing *Pythium debaryanum* and saprophytic organisms than in soil without saprophytes (14); and *e*) have promoted the growth of *Trichoderma viride* in soil by carbon disulphide and succeeded in killing *Armillaria mellea* on infected roots by this method (7).

It is still uncertain, therefore, whether any practical control can be worked out which would be more effective than those now in use. The soil, with all its living microflora, is so complex in composition that any slight variation might occasion failure in a simple biological control attempt. Even the content of soil colloids is capable of inducing changes in the virulence of a pathogen, as was demonstrated for *Pythium debaryanum* (20). All this leads to the conclusion that each type of soil must be studied individually and that for each variation a proper treatment must be determined.

Evaluation of biological control against pathogens attacking the above-soil portions of trees appears to be hopeless because we are far from being able to answer many questions concerning the rivalry of micro-organisms growing on them. Certain laboratory data regarding the Dutch elm disease and chestnut blight fungi demonstrate that these pathogens are susceptible to some micro-organisms under artificial conditions, but to induce such antagonism in nature is certainly more difficult. For effective action a number of conditions must be fulfilled, primarily: *a*) that the antagonist be able to grow on a particular portion of the tree—

bark, wood or leaves; *b*) that its growth or reproduction be faster than that of other parasitic organisms; *c*) that the antagonist produce on these particular areas an active and stable substance; and *d*) that this substance be not toxic to the plant itself.

We can not yet state with assurance that inoculation with certain actinomycetes or with different strains of *Bacillus subtilis* or *Penicillium* sp. on the bark or wounds of valuable chestnut trees would prevent or slow down the development of *Endothia parasitica*; and if such assurance were available, the next and probably most troublesome phase of the problem would still await solution—that of widespread application. Until now, the prospects have been purely hypothetical.

The third aspect of our subject is that of applicability to wood. Use of chemicals for wood preservation is so safe and easy that a biological method of preservation would appear to be unnecessary for many manufactured products. Nevertheless, there are some important problems of wood preservation where chemicals are not effective, namely, in temporary preservation of logs in forests and other storage. Observations on *Trichoderma viride* and *Penicillium crustaceum*, inhibitory saprophytic fungi, reveal that biological protection in such cases might be not only more economical but also more effective than superficial chemical treatment. Here, too, the ample reproductive capacity of the micro-organisms provides the principle reason for considering antagonism in lieu of chemicals, for the organisms may spread along newly created pathways (cracks) formed during the drying period, which chemicals would not do. Lindgren's success in inducing heavy *Trichoderma* infection and thereby delaying decay by spraying wood with fluoride, has been encouraging in assessing the advisability of biological control in forest products.

Many problems still remain to be attacked, and additional information must be gathered on others that have been submitted to investigation, before any final judgement can be passed on the likelihood of extending the great efficacy of antibiotics in combatting human diseases to controlling those of forest trees and lumber products. Several possibilities in applied biology, such as more or less easy introduction of mycorrhizal fungi into poor soils, give certain assurance that biological control of some forest pathogens is realizable.

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THE MEDULLOSAN PTERIDOSPERMS

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INTRODUCTION

Among the members of the Pteridospermae (Cycadofilicales), the genus *Medullosa* is one that has figured prominently in the literature concerned with Paleozoic floras. That stem genus, assigned to the family Medullosaceae (which also includes the stem genera *Sutcliffia* and *Colpoxylon*) is typified by the presence of several stelar axes running through the stem (Fig. 1). This feature distinguishes the Medullosaceae from the Lyginopteridaceae and the Calamopityaceae, the other two families of Paleozoic pteridosperms. Each of the vascular axes (referred to subsequently as "steles", with notes concerning their morphology reserved for a later page) consists of a central body of primary xylem, surrounded by secondary wood, a cambium and phloem. The primary xylem is rather constant in structure among all the representatives of the genus, consisting of large tracheids interspersed among parenchyma cells. As a rule, these tracheids extend vertically, but a variation is to be found among some of the stem types of the European Permian where the primary tracheids almost always assume a horizontal course (Rudolph, 1922). Secondary xylem is composed also of large tracheids, among which radiate tall rays. The extent of development of secondary tissues is not always the same in the various species of *Medullosa*, and often more secondary development is to be found extending toward the center of the stem than on the outer face of the stele. Such a condition was termed "endocentric" by Schopf (1939b) to differentiate it from an "exocentric" configuration where the reverse holds true. Phloem, when preserved, can be seen to

[1] Much of the preparation of this review paper was undertaken while the junior author was a Rockefeller Fellow in the Natural Sciences of the National Research Council.

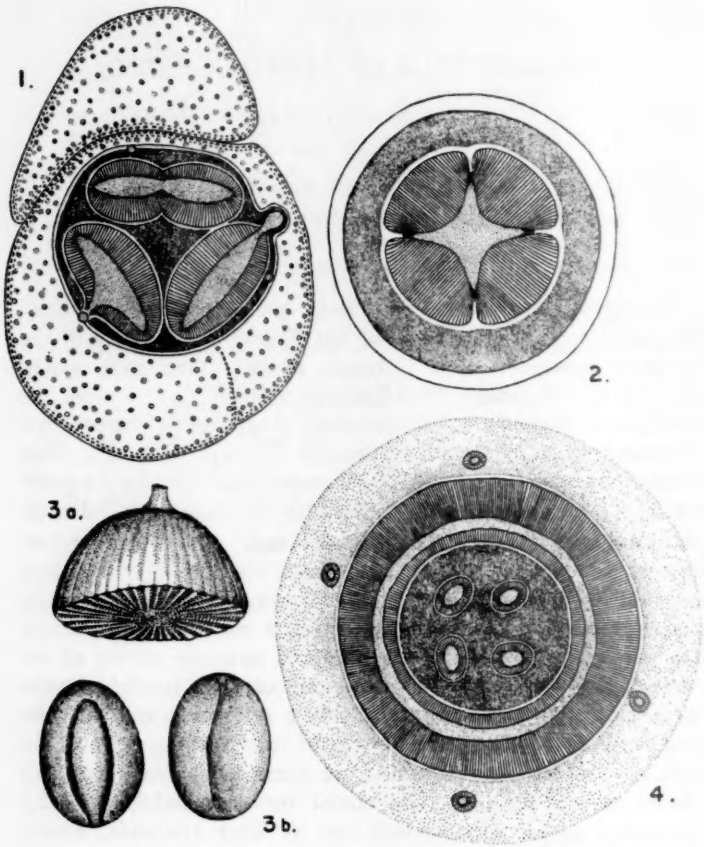


FIG. 1. An idealized cross-section of "typical" three-steled *Medullosa* (based on *M. Noei*). The stele at the top is shown at a level just below stelar branching. Leaf traces are represented by small stippled circles; an adventitious root is shown at its point of origin in the upper right portion of the figure. A zone of internal periderm (clear area bounded by two solid lines) surrounds the steles and the ground tissue. Leaf bases around the stelar system contain leaf traces, secretory canals (small circles) and sclerenchyma strands. The one at the top has been delimited from the rest of the cortex by sclerenchyma.

FIG. 2. Diagrammatic cross-section of a typical medullosan root. A patch of protoxylem (solid black) is at the tip of each of the arms of the protostele. Secondary tissues are not abundant along the "flat" faces of the metaxylem. Surrounding the stele is a zone of parenchymatous cortex, with the root limited externally by a layer of periderm.

consist of sieve cells, phloem parenchyma and rays which are wider at the periphery of the phloem.

The steles in all species are imbedded in a parenchymatous ground tissue which in young stems is surrounded by a band of cells of secondary origin (Fig. 1). This layer is most commonly referred to as an "internal periderm" by most authors. Such a designation is fitting in younger stages, since the leaf bases surround it. The leaf bases at their lower extremities form an encasing layer which can be compared to the cortex of most young plants (Fig. 1). At the periphery of these young stems are vertically extending strands of sclerenchyma fibers which very probably contributed to the support of the plants.

Leaf traces are often small strands of xylem and phloem which originate from the steles, pass through the internal periderm in their upward arching course (Fig. 1), and enter the cortex or leaf bases. Also found in the leaf bases are vertically extending secretory canals (Fig. 1). At a level below the point of separation of a leaf base, it is delimited by sclerenchyma which "cuts" into the cortex and eventually surrounds the entire leaf base (Fig. 1). It is along such a face that the leaf base separates at a higher level.

Adventitious roots are commonly found attached to medullosan stems (Fig. 1). They have a horizontal course at their upper extremities (Scott, 1899; Stewart, 1951a) and bend downward at the stem periphery. Diarch to pentarch protostelic roots are known (tetrarch is the most common type among the American species); secondary elements seem to be concentrated along the flat faces of the primary xylem, and wide rays usually alternate with the arcs of secondary xylem (Fig. 2).

The genus *Medullosa* has been known for well over a hundred years (established by Cotta, 1832), but only gradually have paleobotanists been able to assign other fragments of vegetative plant remains and fertile structures to these tree-like plants.

FIG. 3. a. Restoration of a campanulum of *Dolerotheca formosa*, based on a specimen in the Paleobotanical Collections, Department of Botany, University of Illinois. b. *Monoletes* spores isolated from *Dolerotheca formosa*.

FIG. 4. Diagrammatic transverse section of *Medullosa stellata*. In this specimen a single continuous stelar cylinder surrounds a number of smaller stelar strands in the internal ground tissue. Leaf traces possess secondary vascular elements. After Weber and Sterzel (1896).

The petioles of the medullosae, when found isolated, are known under the name *Myeloxylon.* On them foliage of the *Alethopteris* and *Neuropteris* types were borne, and in some cases leaf types such as *Linopteris, Odontopteris, Lonchopteris,* and perhaps even others belonged to *Medullosa.* The most common petrified male fructification in this country which is considered to possess medullosan relationships is *Dolerotheca* (Fig. 3a), although such synangial fructifications as *Codonotheca, Whittleseya* (Fig. 7), *Aulacotheca, Potoniea, Goldenbergia* and others are also thought to belong to the Medullosaceae. Seeds grouped in the so-called "Trigonocarpales" (usually large, often three-angled seeds) are most commonly referred to the medullosae. Fructifications are discussed in greater detail in a later section.

In spite of attempts to unravel the morphological intricacies and possible phylogenetic significance among the medullosan pteridosperms, only comparatively recently have workers with the group begun to understand these unusual Paleozoic seed ferns. In Cotta's (1832) original description of the genus, in which he established three species, he considered *Medullosa* to be the most troublesome of those encountered by him. Additional material found by later workers from the European continent did little to clear many of the problems connected with the genus, but complicated them somewhat by providing an additional variety of types. Petrifactions of medullosan remains from the British Isles (Scott, 1899, 1914; de Fraine, 1914) revealed stem structures of a still different type. The even more recently discovered *Medullosa* specimens from North America all seem to resemble more closely the British species than those of the European Permian. Perhaps a history of investigations of the genus *Medullosa* will serve to record the progress made by workers with this group.

STEM STRUCTURE

The first specimens of *Medullosa* to be described (Cotta, 1832) originated from the Rotliegende (Lower Permian) of Chemnitz. *Medullosa porosa, M. stellata* and *M. elegans* were distinguished by Cotta in his "Dendrolithen". The last of these, however, was later shown to be merely a petiole, when Brongniart (1849) established the genus *Myeloxylon* for Cotta's *Medullosa elegans.*

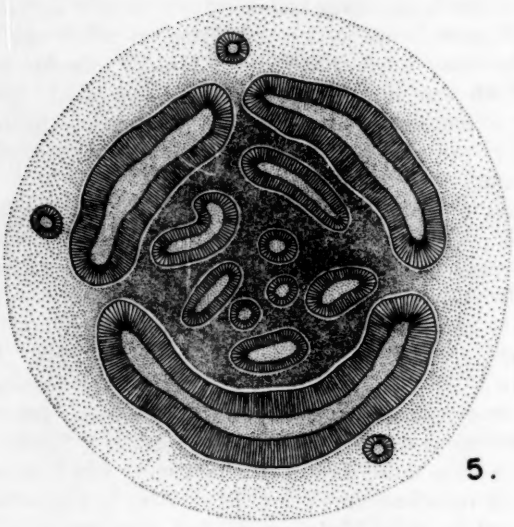
Stems of *M. stellata* have a large hollow cylindrical stele surrounding a mass of parenchymatous ground tissue, in which are imbedded few to many small cylindrical protostelic vascular axes (Fig. 4). Both centrifugal and centripetal secondary xylem radiate from a continuous, or sometimes interrupted, primary xylem cylinder. In this species leaf traces possess secondary vascular elements.

The structure of *M. porosa* is essentially that of *M. stellata*, differing in the presence, in *M. porosa*, of a more regular arrangement of the central steles which are often aligned in one or more rings within the peripheral cylinder. Often, the steles in the cycle just within the outer cylindrical one are strongly endocentric, completely lacking centrifugal secondary vascular elements. The type material of *M. porosa* is also from the Rotliegende of Chemnitz.

Goeppert's study of the Permian fossil flora (1864–5) presents additional descriptions of *M. stellata* and *M. porosa*. Specimens (some of which were those investigated by Cotta) which showed minor structural variations were placed in varieties by that author. A third species of the genus *Medullosa, M. Leuckartii,* was founded by Goeppert and Stenzel in 1882 from material from the Permian of Saxony. This latter species was described in more detail by Solms-Laubach (1897). Several tangentially extended peripheral steles surround a larger number of smaller, more nearly cylindrical, or only slightly expanded tangentially, steles (Fig. 5). In cross-section the contours of the larger outer steles often appear sinuous. In their original description of *M. Leuckartii*, Goeppert and Stenzel illustrated one stem fragment which they considered to show branching of the main axis. It was shown subsequently, however (Solms-Laubach, 1891), that the supposed "branch" was nothing more than a petiole.

Schenk, in 1889, recognized *M. Solmsii* as a species differing from the preceding ones. In this form there are usually two cycles of tangentially expanded steles (not so conspicuously expanded as in *M. Leuckartii*, however) which surround the central ground parenchyma, in which are imbedded a number of small cylindrical vascular strands. This species also originates from the Lower Permian of Europe.

In 1896 appeared a rather significant contribution on the subject when Weber and Sterzel published their still impressive mono-



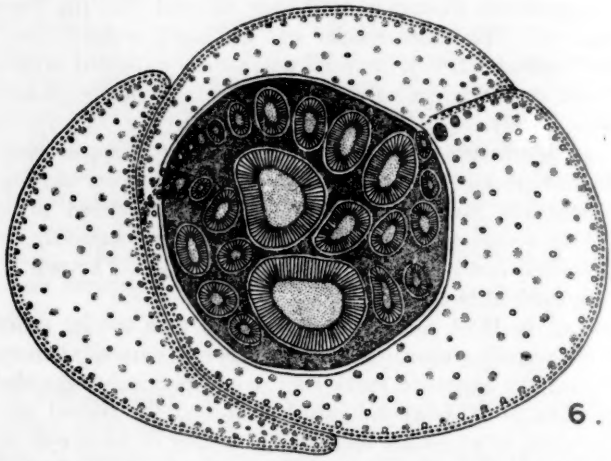


FIG. 5. Diagrammatic cross-section of a stem of *Medullosa Leuckartii*, based on a peel in the Paleobotanical Collections, Department of Botany, University of Illinois.

FIG. 6. Transverse section of *Medullosa primaeva* at a level with many steles, some of the leaf traces accompanied by secondary elements. Based on a specimen in the Paleobotanical Collections, Department of Botany, University of Illinois.

graph of the then-known forms. In addition to their detailed descriptions of the four species, they recognized minor differences within each of the species and established varietal divisions to include deviations from the usual or "typical" configurations. Each of these species, together with the many varietal entities, was the basis for one of their four "form-cycles" (Formkreise). Although these "form-cycles" facilitated the grouping of the Permian medullosae which were known from the European continent at that time, no phylogenetic or evolutionary significance was attached to them, and they served merely as artificial taxa.

Medullosa gigas, described by Renault (1893, 1896), has the most secondary xylem of any of the species (45–50 cm. in thickness), but this specific category is based only on fragmentary material, and it may even be only an old growth stage of *M. stellata.*

All of the stem remains of the genus *Medullosa* which had been described up to that time were from Permian deposits, and all originated from the European continent. Scott's (1899) report of *M. anglica* from the Lower Coal Measures of Great Britain was the first of a specimen from Carboniferous strata. This species, in addition to revealing a member of the genus from an older horizon, presented an anatomical construction conspicuously different from the previously known types (it is not too unlike the type in Fig. 1). Three or four steles is the usual number of *M. anglica,* with no indication of concentric arrangement of the vascular cylinders. Leaf traces in that species are accompanied by secondary vascular elements.

This report was followed in 1914 by another species described by Scott (*M. pusilla*) from the Lower Coal Measures of Lancashire. The main difference between this latter taxon and *M. anglica* is the conspicuously smaller dimensions of *M. pusilla.* Furthermore, secondary elements are absent from leaf traces of *M. pusilla.* In the same year, Miss de Fraine (1914) added another species, *M. centrofilis,* which is typified by three steles surrounding a central one. This specimen also originated from the Lower Coal Measures of Lancashire. Miss de Fraine attached much significance to this central stele in attempting to correlate the Carboniferous types with the larger Permian forms. That stele was homologized with the "star rings" so common in the Continental species, and in this suggestion Miss de Fraine

was followed by several other authors, e.g., Seward (1917), Scott (1923) and Baxter (1949).

In addition to her description of a new species, Miss de Fraine felt that the forms of *Medullosa* known from the British Isles up to that time seemed to constitute a natural assemblage which differed as a group from the Permian types. She proposed a fifth "form cycle" to include the British species, with *M. anglica* serving as the "type".

It was not until 1920 that the genus was reported from the North American continent, when Thiessen (1920a, b) illustrated specimens, Upper Pennsylvanian in age, from southeastern Nebraska (see Andrews, 1945) which he called *M. anglica*. Actually, little concerning detailed anatomical features could be discerned from these specimens, since they were preserved chiefly in pyrite. Schopf (1939b) later placed this form in the variety *Thiessenii* of *M. anglica*.

The first new American species, *M. Noei*, was named by Steidtmann in 1937, and described in more complete detail in 1944. Steidtmann's material was from coal balls found at Calhoun, Illinois, and is Upper Pennsylvanian in age. The stelar number of Steidtmann's specimens ranges from three to four, and in cross-section the steles appear conspicuously expanded in the tangential direction. This species is also characterized by prolific development of periderm or secondary parenchyma.

Since the report of *Medullosa Noei*, remains of the genus have been uncovered with increasing abundance from American deposits. *Medullosa distelica* was established as a new species by Schopf (1939a, b) on the basis of the constant stelar number (two) and on what he considered differences in histological details. Schopf's material was found near Nashville, Illinois, and is Upper Middle Pennsylvanian in age.

Coal-ball material from the Des Moines series in Iowa presented a different type of stem which Andrews (1945) called *M. Thompsonii*. The rather small steles varied from two to three in number, and the leaf bases surrounding the central part of the stem showed features which differed from previously described forms (e.g., fewer vascular bundles, absence of sclerenchyma on the stem above the position of separation of a leaf). A little later, Andrews and Kernen (1946) described a rather fragmentary

specimen, which had only the stelar portion preserved, as a variety of *M. anglica* (*M. anglica* var. *ioensis*). In that specimen three steles were present throughout the length preserved. This specimen also came from the Des Moines series of Iowa.

In 1949 Baxter completed an intensive study of the medullosae, in which he presented three additional species. *Medullosa primaeva*, from the Des Moines series of Iowa, was the first of the forms from this country which showed a rather large number of steles (up to eight), and it was considered by that author to represent a primitive type among the Medullosaceae. *Medullosa elongata* (Des Moines series in Iowa) was differentiated on the basis of the presence of what Baxter supposed to be extremely endocentric, tangentially expanded, steles, and by a general dorsiventrality of the stem fragment. *Medullosa endocentrica* is a small stem type with two conspicuously endocentric steles (no centrifugal secondary vascular elements are present) and with a third small stele. The single specimen on which that species was based by Baxter originated in Illinois in deposits Upper Pennsylvanian in age

In addition to his description of three new species and additional notes on *M. Noei*, Baxter attempted to show relationships among the known forms of the Medullosaceae. He also showed variations which can be found in medullosan steles and suggested a homology among " star rings " (small steles in Permian members), " aggregate leaf traces " (Baxter, 1949), of *M. Thompsonii* and the so-called " periderm rings " of *M. Noei*.

Stewart (1951a) reported a two-steled specimen of *Medullosa* from the Upper Pennsylvanian of Illinois, which he considered different from the earlier-known members, and named it *M. pandurata*. That author also suggested certain revisions in Baxter's proposed phylogenetic scheme of the medullosae.

Scott (1923) suggested the name *Medullosa geriensis* for some specimens labeled *Heterangium geriense* in the Renault collection in Paris. Since that note does not constitute valid publication of that species name, Boureau (1951) formally suggested the name *M. geriensis* with a diagnosis and illustrations. The material illustrated is far from complete, and because of the fragmentary nature of the specimens as well as the lack of significant anatomical differences between that species from the Upper Coal Measures

of the region near St. Etienne and *M. anglica,* Delevoryas (1955) considered *M. geriensis* to be synonymous with *M. anglica.*

Up to 1952, all of the species and varieties of *Medullosa* which had been found in America were from Pennsylvanian deposits (Middle to Upper Pennsylvanian). Roberts and Barghoorn (1952), however, described *M. Olseniae* from deposits in Texas which are Permian in age. Unfortunately their material is rather fragmentary, and complete details of the structure of that species are wanting. From their fragments it is obvious that the stelar number of that species ranged from three to five, and stelar branching, although present, was infrequent. The steles are usually somewhat expanded tangentially.

In 1952, a rather striking specimen was described by Stewart and Delevoryas from a coal ball from southeastern Kansas (Middle Pennsylvanian). In that specimen is a remarkable variation in stelar number throughout the preserved length. At the lowest level in the stem fragment, two steles are present, but higher in the stem there occurred prolific ramification of steles resulting in as many as 23 (Fig. 6). Some of the branch steles functioned as leaf traces, while others fused, and still higher a smaller number, probably two, was reconstituted. The authors differentiated their specimen, which they called *M. heterostelica,* from *M. primaeva,* which also has many steles, on the basis of the presence of secondary vascular elements on leaf traces of *M. heterostelica,* while none was reported for *M. primaeva.* In the same paper these authors outlined a scheme suggesting phyletic trends within the Medullosaceae based on conclusions derived from the study of *M. heterostelica.*

Andrews and Mamay (1953) reported a number of rather well-preserved stem fragments of *Medullosa,* among which was a single specimen which they designated as *M. grandis.* This specimen, from the same Kansas locality, is the largest in diameter of all the stem fragments from this country. It is characterized by a large number of steles throughout its length, although there is some stelar fusion at the upper levels of the coal ball. The steles are large, and there is considerable development of secondary parenchyma throughout the stem. Other specimens which Andrews and Mamay describe and figure are two which they assign to *M. Thompsonii,* one to *M. heterostelica,* one to *M. dis-*

telica (all from the Middle Pennsylvanian of Kansas), and one to *M. Noei* (Upper Pennsylvanian of Illinois).

The most recent extensive investigation of the medullosae is that of Delevoryas (1955) which is the result of an examination of all of the specimens described in this country up to that time, together with a study of many previously undescribed stem fragments. As a result of this investigation, the author has been able to trace the development of a stem of *M. Noei* from a level near the apex to a nearly basal portion. A young region of this species is characterized by small steles—both the primary and secondary portions—and by the presence of leaf bases surrounding the inner part of the stem. As that region of the stem became older, there was an increase in thickness of secondary xylem and phloem, as well as of internal periderm, which changes are to be expected. Still further secondary growth resulted in the sloughing off of leaf bases and other primary cortical tissue external to the periderm. This left the stem surface covered by parenchyma-like periderm which in old stages became rather thick and irregular.

In all of the specimens of *M. Noei* examined by Delevoryas, there is a very definite relationship between size of primary xylem and extent of development of secondary wood. When the primary xylem has a small cross-sectional area, secondary xylem is correspondingly slightly developed, and this condition invariably occurred in a young stem portion. With increasingly larger primary xylem there is always more extensively developed secondary wood. This phenomenon would suggest that the primary xylem retained its potentialities for increase in volume, even after the secondary wood had begun to develop. The rather large amount of parenchyma-like tissue within the primary xylem (considered to be persistent procambium by Delevoryas) could have undergone additional divisions to increase the size of the primary xylem. Supposedly "mature" parenchyma cells in other parts of the stem showed such meristem-like characteristics. It might be argued that in the medullosae, as in the lepidodendrids, the size of the primary xylem varied in different parts of the same plant, and those stem fragments with a large amount of primary xylem are basal portions, while those portions with only a small primary portion of the stele came from higher in the plant and never did increase in size. Such a possibility is conceded by

Delevoryas, but only in the case of very small stem axes of *Medullosa*, which have extremely small steles and long internodes. If the primary xylem did not enlarge during the ontogeny of the stem, however, we would expect to find at least a few specimens with primary xylem large in cross-sectional area (a supposedly basal portion), with only a little secondary development. Such a condition is frequently observed among petrified *Calamites* stems. On the contrary, as mentioned above, there is a direct relationship between size of primary xylem and extent of development of secondary vascular tissues. In addition, the presence of the so-called "periderm rings" within the primary xylem gives evidence to the suggestion that the parenchyma in the primary xylem was capable of undergoing divisions in older stages. Subsequent divisions of parenchyma cells in the rays could easily have accommodated any change in outline of the mass of secondary vascular elements of any increase in circumference of the internal surface of the secondary xylem necessitated by the expanding primary xylem.

Thus, with a knowledge of the various stages of development of *M. Noei*, Delevoryas (1955) concluded that certain of the species which had been established by previous workers, can be interpreted as growth stages of *M. Noei*. Those "species" which have been reduced to synonyms of *M. Noei* are *M. distelica* Schopf (1939a, b) and *M. pandurata* Stewart (1951a). Although the name *M. endocentrica* Baxter (1949) was retained, it was suggested that the single specimen described by Baxter is merely an apical portion of *M. Noei*.

In addition to the study of fragments of *M. Noei*, Delevoryas (1955) assembled a considerable number of specimens from Kansas and Iowa localities, beside re-examining the specimens described from these collecting sites by earlier authors. Further study of the specimen named *M. heterostelica* Stewart and Delevoryas (1952) showed that in certain parts of the stem, especially where the steles were not undergoing branching (but not confined to those areas), leaf traces are entirely primary. For that reason it is now impossible to distinguish *M. heterostelica* from *M. primaeva* Baxter (1949) which was described as having leaf traces with no secondary development. With the rest of the specimens from Kansas and Iowa, some knowledge was gained

concerning the sequence of development in *M. primaeva,* and as a result, other previously named forms can be considered synonymous with that species. In addition to *M. heterostelica,* the specimens called *M. Thompsonii* and *M. distelica* from Kansas in the paper by Andrews and Mamay (1953), *M. grandis* Andrews and Mamay (1953) (an old stage of *M. primaeva*), *M. elongata* Baxter (1949) (a badly crushed stem fragment), *M. anglica* var. *ioensis* Andrews and Kernen (1946) are all treated as various growth stages of *M. primaeva.* Enlargement of primary xylem seems to have occurred in *M. primaeva* during the ontogeny of the steles, but not to so great an extent as in *M. Noei,* in which form tangentially expanded steles characterize the older stages. In the largest specimen of *M. primaeva* described thus far (*M. grandis* of Andrews and Mamay), some of the steles are considerably "elongated" in cross section, while other, smaller ones retained their cylindrical configuration. This feature was considered of some importance by Delevoryas in attempting to formulate the pattern of evolution within the genus.

Besides *M. Noei* and *M. primaeva,* the species and one variety of *Medullosa* from North America recognized by Delevoryas (1955) are: *M. anglica* var. *Thiessenii* Schopf (1939b) (retained by Delevoryas because of the fragmentary nature and peculiar mode of preservation of that specimen which prevent an accurate diagnosis of all characters), *M. Thompsonii* Andrews (1945), *M. endocentrica* Baxter (1949) (retained on a provisional basis), and *M. Olseniae* Roberts and Barghoorn.

It was estimated by Andrews and Mamay (1953) that the number of species and varieties of *Medullosa* which had been described up to that time was 44. It at once becomes obvious that there certainly must have been considerable duplication, and it was to be expected that a more thorough knowledge of the structure of medullosan stems in their entirety would eventually lead to a diminution in the number of specific entities recognized by earlier workers. Those workers were perhaps justified, to some extent, in establishing the large number of species and varieties which are found in the literature up to the present, since it has only been in recent years that a greater amount of material has become available for study. As was pointed out by Delevoryas (1955), a study of fern anatomy is complicated by a change in structure

at increasingly higher levels. This same problem is encountered to some extent among the medullosae, since the internal structure may vary considerably at different levels in the stem. This difficulty is complicated by the superimposition of secondary development. As a result, corresponding levels in two stems of the same species might show a difference in structure if both of the plants were not of the same age.

Furthermore, certain of the stages in development in *Medullosa* stems indicate that it is not always possible to interpret these plants, and many other types of fossil plants in addition, on the same bases used for extant floras. Paleobotany has been retarded, to some extent, by our inability to apply the concepts gained from a study of plants living at the present, to fossils with an entirely different mode of growth.

LEAF BASES AND LEAVES

A re-examination of Cotta's (1832) species of *Medullosa, M. elegans,* led Brongniart (1849) to establish the genus *Myeloxyon* for it, although he did not at that time realize that it was actually a petiole of *Medullosa* with which he was dealing. *Stenzelia* was the name proposed by Goeppert at a later date (1864–5), since he did not agree with Brongniart's opinion that the genus had monocotyledonous structure. Renault (1876) suggested the name *Myelopteris,* instituting the combination *Myelopteris radiata* for Cotta's *Medullosa elegans.* This step was taken by Renault because he believed those structures to be fern-like, although Binney in 1872 (Seward, 1917) had previously suspected a petiolar nature for them. Schenk (1882) suggested a retention of the name *Myeloxylon,* since there was no valid reason for doing otherwise, and stated that if the name were to be changed, Goeppert's *Stenzelia* took priority over *Myelopteris.* The true nature of the axes which were known by these various names was noticed by Grand'Eury (1877) who saw similarities in structure between rachises of certain foliage types and *Myeloxylon,* although at that time he applied the name *Aulacopteris* to those petioles. It was Solms-Laubach (1891) who suggested that *Myeloxylon* was actually a medullosan petiole. It is somewhat ironic that *Medullosa elegans,* one of the species named by

Cotta, for which the genus *Myeloxylon* had been established, should turn out to be a petiole of the genus *Medullosa* after all of the previous misinterpretations.

As suggested by Seward (1917), it should be unnecessary to retain a separate name for organs known to belong to *Medullosa*. On the other hand, the fact that so many of such petioles are found isolated and cannot be assigned to the proper *Medullosa* species would favor retention of the form-genus *Myeloxylon*.

Myeloxylon radiatum (Renault) Schenk (*Myelopteris radiata* of Renault, 1876) was established to include *Medullosa elegans*, although Zeiller (1890) suggested that Cotta's *Medullosa elegans* be treated as a distinct species. The absence of rules of nomenclature as we know today has been responsible for a certain amount of confusion concerning authorship of some of the species of *Myeloxylon*. Although Schenk (1882) never actually used the combination *Myeloxylon radiatum*, he certainly meant to include Ranault's *Myelopteris* in the genus *Myeloxylon*, the earliest one used for medullosan petioles. For that reason he may be considered the author of the combination *Myeloxylon radiatum*. Petioles of the *M. radiatum* type are sometimes found attached to stems of *Medullosa Leuckartii*.

A similar situation prevails concerning the combination *Myeloxylon Landriotii* (Renault) Schenk which was differentiated by Renault (1876) on the basis of a more nearly circular cross-section of the sclerenchyma patches at the periphery of the axis, as opposed to the radially expanded groups in *M. radiatum*. Petioles of *Medullosa anglica* resemble *Myeloxylon Landriotii*.

Penhallow's (1897) description of *Myeloxylon topekense* was the first report of the genus from the Western Hemisphere. Penhallow used Renault's *Myelopteris* in referring to his material, and, as far as the present authors have been able to determine, Seward (1917) was the first to use the proper combination, making him the authority for it. The somewhat tangentially expanded patches of sclerenchyma were considered to be sufficient basis for separating it from the European forms, although the preservation of Penhallow's material was rather poor.

Myeloxylon missouriensis Arnold and Steidtmann (1937) has small sclerenchyma strands, often in double rows. According to

Steidtmann (1944), it differs from his *M. zonatum* (Steidtmann, 1944) in which there is a zone of vascular bundles and secretory canals inside the peripheral sclerenchyma zone.

Still another species of *Myeloxylon*, *M. Bendixenii*, was established by Andrews (1945) on the basis of a thick "rind", more abundant association of secretory canals with sclerenchyma strands, and the absence of a sharp line of delimitation of the inner bundles of the "rind".

In his 1955 paper, Delevoryas suggested the hazards involved in naming species of *Myeloxylon*, or using leaf base characters as aids in the identification of *Medullosa* stems. As in stems, there seems to have been a series of changes which took place in leaf bases (or petioles) with increasing age. Secretory canals enlarged considerably in older leaf bases, and there also seems to have been an increase in the amount of sclerenchyma. Secretory canals are also formed in later stages, interspersed among the sclerenchyma strands, although they may have been absent from that region in younger stages. Delevoryas suggested that, as in stems of *Medullosa*, petioles apparently contained parenchyma cells which were capable of undergoing divisions in the ontogeny of the petiole to form more sclerenchyma. One specimen of *Medullosa Thompsonii* described by Delevoryas had a leaf base which had been penetrated by a *Psaronius* root. As a reaction to this wound, parenchyma cells in the vicinity underwent divisions resulting in a seriation of those cells, together with an interruption of sclerenchyma strands both in the leaf base and at the stem periphery at that area. Holden (1910) reported a wounded *Myeloxylon* in which many of the parenchyma cells became rejuvenated (or perhaps some of their meristematic potentialities were realized), forming wound tissue which very much resembles periderm. In support of his argument, Delevoryas showed a series of photographs of leaf bases in progressively older stems of *Medullosa primaeva*, and there is a striking transition from leaf bases with few, small sclerenchyma strands, with minute and few secretory canals, to leaf bases with large conspicuous sclerenchyma strands, with a greater number of larger canals. Often the extent of crushing of the organ greatly influences the final configuration of the tissues in a *Myeloxylon* axis.

Until there is a correlation of internal structure of leaves in

petrified material with the many types of compressed foliage, any attempts to list the types of leaves borne by the medullosae must be only tentative. *Alethopteris* and *Neuropteris* leaf types are those most generally assumed to belong to *Medullosa*, and it is possible to identify these two genera, with a great degree of certainty in coal balls, since occasionally a fractured face of a coal ball reveals these two types of fronds. *Odontopteris* fronds are known to possess rachises resembling *Myeloxylon* (Seward, 1917) and for that reason are also considered to have been borne by some species of *Medullosa*. *Linopteris*, *Lonchopteris* (Arnold, 1947), *Callipteris* and even *Taeniopteris* (Seward, 1917) foliage types are often regarded as medullosan. As was suggested by Seward (1917), however, the mere presence of *Myeloxylon*-type rachises can not be used as certain proof that the leaves are medullosan, since other petiolar types are superficially similar.

More must be known about the fronds in their entirety to allow accurate reconstructions, although Andrews (1945) figures a drawing of *Alethopteris* in which the rachis underwent unequal bifurcations. Bertrand (1932) and Kidston (1911) show that such a feature is present in at least some of the frond genera. Delevoryas (1955) observed in coal-ball material that axes of *Myeloxylon* underwent equal, or slightly unequal, branching, at least in their lower portions, and it is not until the more distal regions of the fronds that a regular pinnate arrangement is attained.

FRUCTIFICATIONS

There is even less certainty in the fructifications of true medullosan affinity than prevails among the leaf types. In fact, the usual evidence used to determine the medullosan nature of fructifications is their attachment to, or close association with, leaf types thought to belong to *Medullosa*. A great variety of microsporangial types exists which are considered to be medullosan, and in almost all instances these fructifications are synangial in nature. Furthermore, the spores found in almost all of these reproductive structures are those called *Monoletes* (Fig. 3b).

In 1887, Kidston reported a specimen of *Neuropteris heterophylla*, some of the terminal branchlets of which were thought to bear small four-valved sporangia. Bertrand (1913) suggested the name *Neurotheca* for these supposed pollen-bearing organs.

Halle, in 1933, completed a rather impressive monograph of spore-bearing organs of the pteridosperms. With careful techniques he was able to determine the three-dimensional appearance of these compressions. He divided these structures into two groups: the Whittleseyinae and the Potonieinae. Genera in the first group he suggested belong to certain *Alethopteris* and *Lonchopteris* species, in addition to the imparipinnate sections of *Neuropteris* and *Linopteris*. The *Potonieinae* probably are assignable to the paripinnate neuropterids.

Codonotheca Sellards (1903) (Whittleseyinae) is a narrow, cup-shaped structure with six, free, linear, fertile segments. On the basis of its association with *Neuropteris decipiens*, Sellards was inclined to consider *Codonotheca* a pteridosperm fructification, probably of *Medullosa*.

Goldenbergia Halle (1933) is a truncated, obovoid, seed-like synangium which has a series of long tubular sporangia surrounding the hollow interior. *Aulacotheca* Halle (1933) consists of several elongated sporangia fused into a hollow ellipsoid. *Whittleseya* is somewhat similar but is larger, with more sporangia, and the entire synangium is urn-shaped. Recently Jongmans (1954) reported *Whittleseya media* in attachment to *Neuropteris Schlehanii* in compression material from the Lower Westphalian A of the Netherlands (Fig. 7).

Boulaya differs from *Aulacotheca* in that it has a continuous spore-bearing zone instead of the several elongated sporangia in the latter. *Dolerotheca* Halle (1933) is a campanulate synangium with the elongated tubular sporangia imbedded in a loose tissue with only the tips exposed (Fig. 3a). *Dolerotheca* specimens are frequently encountered in American coal balls (Schopf, 1948; Baxter, 1949).

Among the Potonieinae, *Potoniea* is a campanulate structure with many narrow elongated sporangia contained within a sterile lamina (Halle, 1933).

Seeds of the Trigonocarpales are generally recognized as being those of the medullosae. Frequently in compression fossils large seed-like structures are actually found attached to the tip of a neuropterid pinna (Fig. 8). Kidston's (1904) report of a seed attached to a frond of *Neuropteris heterophylla* is significant, since it definitely correlated a radiospermic seed with neuropterid foliage.

Jongmans (1954) reported seeds attached to *Neuropteris Schlehanii* in the same material showing the male structure, *Whittleseya*, attached to the identical leaf type. Trigonocarp seeds, many of which in their petrified state are placed in the genus *Pachytesta* (see Hoskins and Cross, 1946), are abundant in Europe and North America. In that genus are perhaps the most commonly occurring

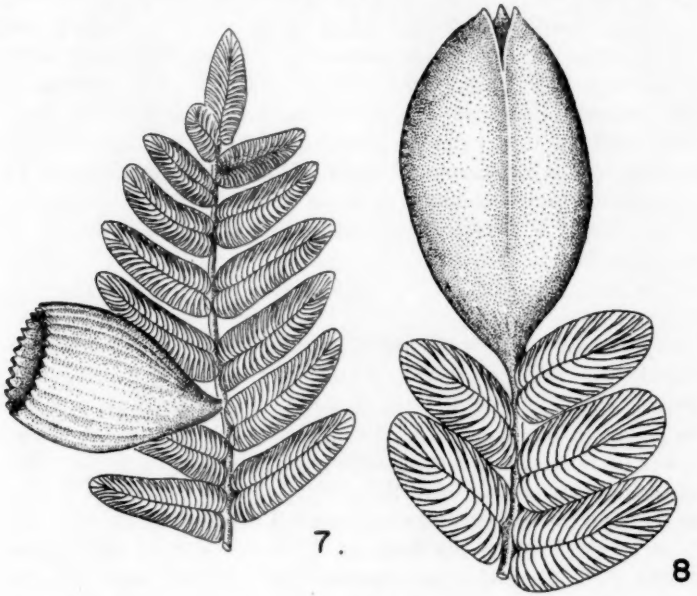


FIG. 7. Restoration of *Whittleseya media* attached to *Neuropteris* foliage. Based on Jongmans (1954).
FIG. 8. Restoration of a seed of the Trigonocarpales attached to *Neuropteris* foliage. Drawn from photograph in Arnold (1947).

petrified seeds considered to be medullosan. In Illinois coal balls, *Pachytesta illinoense* (Stewart, 1954) (formerly *Rotodontiospermum illinoense* Arnold and Steidtmann [1937]) is consistently associated with remains of *Medullosa Noei* and with alethopterid foliage. Furthermore, analysis of the pollen grains in the pollen chamber of that seed reveals *Monoletes* spores which are identical with those in *Dolerotheca formosa* from the same locality (south-

eastern Illinois). As a rule, seeds of the Trigonocarpales are large, having many features in common with cycad seeds. There are, in addition to *Pachytesta*, other similar seeds which differ in minor details which are placed in *Hexapterospermum*, *Aethiotesta*, *Ptychotesta* and other genera (Hoskins and Cross, 1946).

HABIT OF THE MEDULLOSAE

Our ever-increasing knowledge of the structure of plants in the genus *Medullosa* permits reconstruction of one of those plants with a fair degree of accuracy in almost every detail. The restoration by Andrews (1945) was one of the most acceptable for some time, but additional knowledge of growth forms found within a single species necessitates certain changes. With so many specimens of considerable stem diameter, it is no longer necessary to regard *Medullosa* as a vine or a scrambler (Baxter, 1949), since all of the secondary development in a large stem certainly seems capable of having supported an upright stem of appreciable height. Furthermore, Delevoryas (1955) suggested that the "dorsiventrally flattened" stems of *Medullosa* figured by Baxter (1949) are merely mechanically crushed, and a well-preserved specimen shows leaves originating on all sides of the stem. Figure 9 is intended to portray a specimen of *M. Noei* 12 to 15 feet in height. The lower portion is limited externally by periderm, and it is from this region that supporting adventitious roots arise. Somewhat higher in the stem are functionless persistent leaf bases which have not yet been sloughed off by periderm development. Leaves were borne at the apex. Reproductive structures were omitted, but it appears quite probable that *Dolerotheca formosa* and *Pachytesta illinoense* were borne on such a plant.

MEDULLOSAN PHYLOGENY

Since the original description of *Medullosa*, many attempts have been made to determine the relationships of the medullosae, as well as to determine evolutionary trends within the group. Most of the advances made in the interpretation of medullosan stems did not begin until the work of Goeppert and Stenzel (1882) who showed the stems to be composed of a system of more peripheral "flattened" "plate-rings", surrounding the more internal "star-rings". These steles, in the Permian forms known at that time,

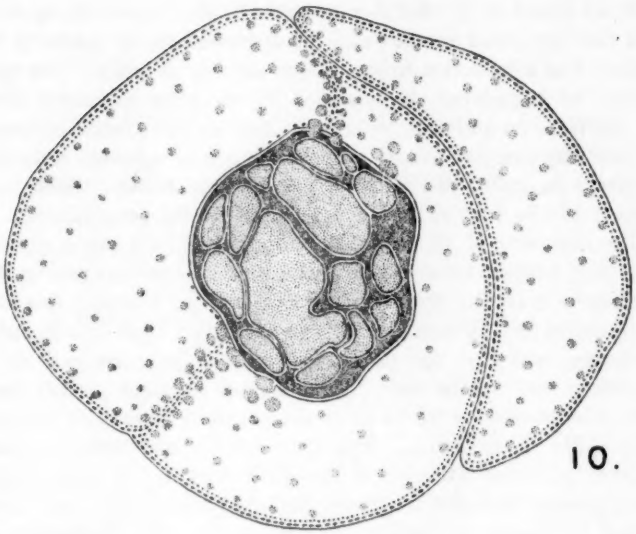
FIG. 9. Suggested reconstruction of a plant of *Medullosa Noei*, 12 to 15 feet in height.

differed from each other only in shape. It was Schenk (1889), however, who observed the presence of primary wood in the center of each of the steles. The polystelic nature of these stems, which had now become evident, was used by Zeiller (1890) as basis for comparison with fern anatomy. Even Weber and Sterzel (1896) were impressed by the apparent similarity between *Medullosa* and certain ferns, and even went so far as to compare the structure of *Medullosa* with the internal anatomy of *Psaronius*. Scott (1899) was attracted by Solms-Laubach's (1896) account of *Cladoxylon*, one of a group of supposed primitive ferns (Cladoxylales), and used the similarity of structure of that genus to medullosan structure as evidence for a fern origin of the latter.

Scott also emphasized the resemblance of medullosan steles to the individual stele in *Heterangium*, as have many subsequent investigators. To carry the analogy to ferns even further, Scott and others considered *Heterangium* to be fern-like in many ways, including the stelar structure (which superficially resembles the stele of some gleichenias) and the frond-like nature of the leaves.

The discovery of another medullosan genus, *Sutcliffia* (Scott, 1906), was the basis for some speculations as to evolutionary trends within the Medullosaceae. The stem of *Sutcliffia* (Fig. 10) is typified by a large central stele, surrounded by smaller ones which grade farther out to smaller leaf traces. Scott (1906) suggested that in that plant is found the primitive type of medullosan structure—one that is essentially protostelic. This view was repeated by Miss de Fraine (1912) when she presented additional observations on the genus *Sutcliffia*. From *Sutcliffia* these workers derived the *Medullosa anglica* type of structure, while the Permian forms were supposed to be still more highly advanced.

Scott's description of *Medullosa pusilla* in 1914 did little to change pre-existing ideas of the development among the medullosae, but in the same year Miss de Fraine reported on *M. centrofilis*, which was considered a different type because of the presence of a fourth stele surrounded by three larger steles. This feature was regarded by Miss de Fraine as showing a transition to the Permian types (Fig. 12). The small central stele was considered homologous with the more abundant star rings of the Continental members. Miss de Fraine's suggestion has persisted in the literature until very recently (e.g., Seward, 1917; Scott, 1923; Schopf, 1939b; Steidtmann, 1944; Baxter, 1949).



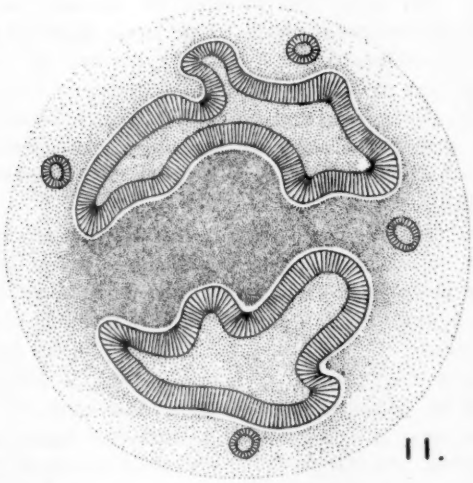


FIG. 10. Idealized cross-section of *Sutcliffia insignis*. Based on Scott (1906) and Miss de Fraine (1912).

FIG. 11. Diagrammatic transverse section of *Colpoxylon aeduense*. After Renault (1893).

In his report on *M. distelica,* Schopf (1939b) was of the opinion that the two-steled condition of his specimen should probably be regarded as a reduction from a larger number of steles. For that reason he considered *M. distelica* to be more advanced than *M. anglica.* In addition, he believed that an endocentric arrangement of the vascular tissues, especially when so apparent as in the specimen he called *M. distelica,* was another feature which was supposed to be derived from a more nearly radial arrangement.

The discovery of *M. primaeva* by Baxter (1949) was a significant step toward some of the more recent ideas concerning the development of the medullosae. That author believed that the many-steled type of medullosan stem originated from a monostelic prototype, and that the polystelic condition was attained by a " proliferation " of the stele. Thus Baxter supposes a small stem with a large number of steles as the primitive type of *Medullosa* (Fig. 13). A fusion, resulting in a smaller and more constant number of steles (three), is an advancement. A progressive development into dorsiventrally flattened stems was also suggested by Baxter as having occurred among the Carboniferous members. His next step involves an increase in size (e.g., *M. Noei*), and eventually leads to the larger Permian forms from Europe. *Medullosa distelica, M. elongata* and *M. endocentrica* were placed in a position by themselves, stemming from somewhere between *M. Thompsonii* and *M. anglica. Sutcliffia* was apparently regarded as having a stelar system which was essentially protostelic, but having resulted from a fusion of a larger number of vascular axes.

Stewart (1951a) modified Baxter's scheme to some extent (Fig. 14). First of all, he believed that a decrease in amount of secondary vascular tissue accompanying leaf traces suggests an advanced feature. For that reason he elevated Baxter's " dead-end side chain " (*M. distelica, M. elongata* and *M. endocentrica*) to a position originating from above *M. anglica* (*M. anglica* has secondary elements on the traces). Stewart's *M. pandurata,* which was thought to have some secondary vascular elements in the leaf traces, was relegated to a position between *M. anglica* and *M. Noei* (with leaf traces entirely primary). Schopf (1939b) did not include *M. Noei* in the Anglorota group, and, since Stewart believed *M. pandurata* to be transitional between *M. anglica* and

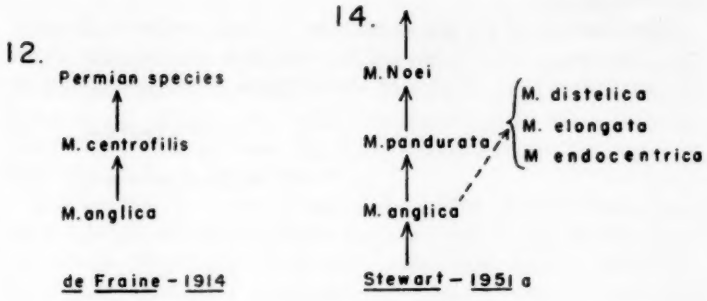


FIG. 12. Evolution within the medullosae as suggested by Miss de Fraine (1914).
FIG. 13. Baxter's (1949) evolutionary scheme.
FIG. 14. Suggested evolution of the Medullosaceae by Stewart (1951).

M. Noei, he expressed the idea that the sub-genus Anglorota is an artificial one.

The discovery of the specimen called *M. heterostelica* by Stewart and Delevoryas (1952) seemed to strengthen the idea that those species with a large number of steles represent the primitive type

FIG. 15. Phylogeny of the Medullosaceae suggested by Stewart and Delevoryas (1952).

of medullosan. One striking feature of their specimen is the formation of certain leaf traces by dichotomies, or near dichotomies, of the stem steles (primal steles of those authors). At progressively higher levels, the traces lost the secondary vascular elements. The authors suggested two main lines of evolution within the medullosae (Fig. 15)—one exemplified by the types with phyletic

fusion of steles (or failure of the steles to undergo divisions) and a decrease in amount of secondary elements on the traces. The other line, which is perhaps the one which led to the cycads, retained secondary elements on the leaf traces, and also in one way or another showed a many-steled condition (e.g., the accessory steles of *M. anglica,* the "periderm rings" in *M. Noei* [at that time these structures were thought to be homologous with steles], star rings in the Permian forms).

In their description of an additional number of *Medullosa* stems from this country, Andrews and Mamay (1953) suggest that there are two possible origins of the many-steled medullosae. One might have been from a two-steled type, the vascular axes of which underwent several branchings to form a type such as their *M. grandis.* The other possibility is that a many-steled ancestral type actually preceded the medullosae (they suggested such forms as *Cladoxylon, Steloxylon, Pietzschia, Xenocladia*—all many-steled stem types—as showing a kind of stelar construction which could possibly have led to the medullosan stem structure). If such were the case, then a fusion of steles would result in the development of the usually three-steled forms. In the latter idea they agree essentially with what was suggested by Stewart and Delevoryas (1952).

The work of Delevoryas (1955), which drastically revised our interpretation of many of the "species" and "varieties" of *Medullosa,* actually changed little of the basic concepts in the earlier paper by Stewart and Delevoryas (1952). The number of species and varieties was reduced considerably (note synonymy earlier in this paper), and this necessitated some revision of the chart used by Stewart and Delevoryas in their paper. In addition, Delevoryas suggested that it is often misleading to attempt to show lines of development in a group of plants by placing one species above the other, connected with a line. This difficulty was remedied somewhat by the suggestion that it may be better to attempt to determine "trends" within the group and to regard the various species and varieties of *Medullosa* as having progressed for varying degrees along these lines. It was suggested by that author that the medullosae probably owed their origin to psilophyte-like precursors—forms composed of leafless dichotomizing systems (Fig. 16). Actually, this idea did not originate at that time, but was expressed earlier. Arnold (1947) recognized the

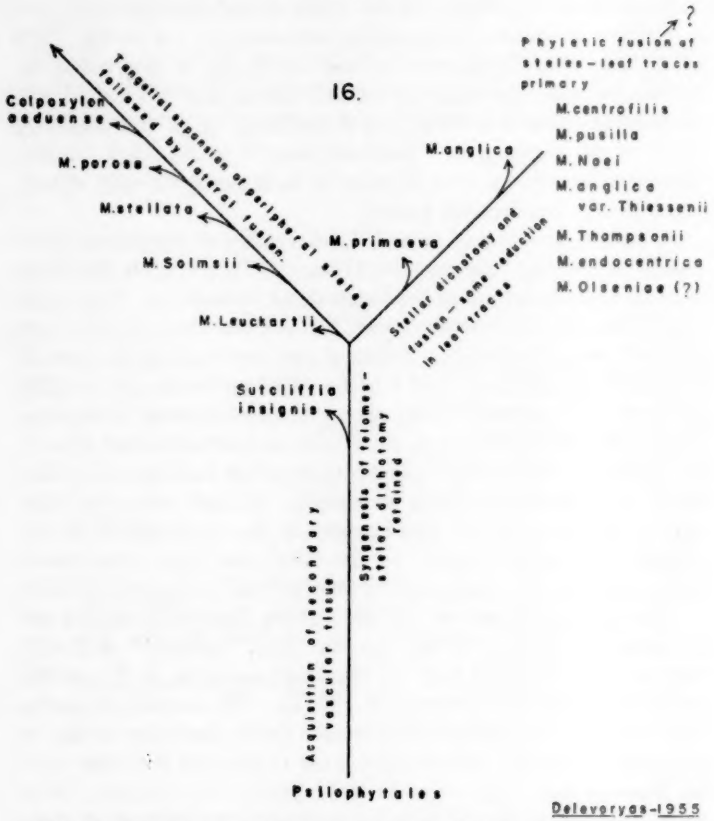


FIG. 16. Evolutionary developments in the Medullosaceae presented by Delevoryas (1955).

possibility that psylophytalean stock was the source of the pteridosperms, although he was more inclined to believe that there was an intermediate heterosporous fern-like complex. In his phyletic chart, Baxter (1949) derived the medullosae from the Psilophytales. Stewart and Delevoryas (1952) interpreted the stem types of *Medullosa* as axes which retained a dichotomizing system, modified, in some types, by ontogenetic and phyletic fusions.

In Delevoryas' (1955) diagram (Fig. 16), the line proceeding from the Psilophytales is one which is characterized by the acquisition of secondary vascular elements (known in some of the Psilophytales) followed by a fusion of some of the axes, but with a retention of the dichotomizing stelar systems (syngenesis of telomes [Zimmermann, 1930]). An anastomosis of the vascular system then followed. At this point Delevoryas recognized two distinct patterns of development—one in which there is a progressive differentiation of leaf traces (characterized by a progressive loss of secondary vascular elements) and a reduction of stelar number (phyletic fusion); the second involves a fusion of steles (but in a tangential direction) to form ultimately a single hollow stele, together with a retention of secondary elements on the leaf traces. All of the Carboniferous members, and *M. Olseniae*, are examples of the first trend, while the European Permian forms had developed along the second line. *Colpoxylon aeduense* Brongniart (Renault, 1893, 1896) has been interpreted as having a stelar system formed by a phyletic fusion (tangentially) of the several peripheral steles of some of the Permian forms originating from the European continent (Fig. 11). The internal "star rings", which in some of the Permian medullosae showed only little primary xylem and were often small in size and number, appear to have disappeared entirely in *Colpoxylon*.

Sutcliffia, interpreted as a protostelic type by Scott (1906) and de Fraine (1912), was treated as an extremely primitive type of medullosan (following the interpretation of Stewart and Delevoryas in 1952), since it possesses a stelar system which had retained many of the characteristics of a form which was suggested by Delevoryas as representing dichotomizing stelar cylinders within fused axes. Even Miss de Fraine (1912), who suggested that *Sutcliffia* is essentially a simple protostelic type, admitted that there is very little difference between the "meristeles" which branched from the central vascular axis, and the stele itself.

In the scheme presented by Delevoryas (for which he does not assume full credit) leaves of the medullosae can then be interpreted as modified branching systems. The more primitive type of leaf is one in which there is little difference between the stem steles and the vascular bundles entering the leaves. A member which appears to show a stem system "caught in the act" of becoming

differentiated into a leaf was described by Delevoryas (1955). In that specimen a lateral branch was observed to originate from the stem. The three steles in that branch had only a small amount of secondary vascular elements, which even decreased at a higher level. In this respect the branch shows no difference from a leaf occasionally present in *M. primaeva* in which the lower portions of the leaf traces are accompanied by secondary xylem and phloem. There is, however, a band of sclerenchyma on that branch which delimits the base of a leaf borne on it. Furthermore, leaf traces arise from the steles in the branch, pass through the sclerenchyma, and enter that leaf base.

Scott (1923) was reluctant to admit the source of the cauline vascular axes, and used the term " steles " merely in the descriptive sense, not implying, thereby, their origin or morphology. Most authors have also used that same term, with no qualification, but in 1952 Roberts and Barghoorn suggested that it is incorrect to refer to the vascular axes as steles, or to use the term " polystele " when describing the entire vascular system of a stem. Those authors regarded the entire primary portion of the vascular system as constituting a single stele. They continued to use the expression " polystele " as a matter of convenience but enclosed it in quotation marks.

Delevoryas (1955) demonstrated the difficulty involved in separating primary and secondary development in each of the vascular axes in a medullosan stem, and, in fact, it seems that primary differentiation continued for a time even after the secondary development had been initiated. It would seem, therefore, that the development of primary and of secondary stelar tissues does involve two distinct processes, but that both are merely activities that result in the formation of the stele.

Strong evidence for the contention that each vascular cylinder can be regarded as a stele is found in the pattern of stelar ramification in *Sutcliffia* and in some specimens of *Medullosa primaeva* where, if each of the vascular cylinders were imagined to be surrounded by its own stem axis, a striking dichotomous system would result. Interpreted on the basis of the telome concept (Zimmermann, 1930; Wilson, 1953), a leaf is nothing but a modified branching system, each of the veins (or vascular bundles) of which is the morphological equivalent of a stele. In such a case

there is never any occasion to refer to the entire vascular system of a leaf as being one stele. Why, then, should not a similar interpretation be applied to the stem of *Medullosa*? In *M. primaeva* there are often cases where a leaf base and stem cross-section are almost identical.

RELATIONSHIPS

The polystelic condition present in *Medullosa*, a rather uncommon type of stelar construction in the plant kingdom, is perhaps mainly responsible for the pre-existing ideas that these plants hold some relationship with ferns. Zeiller (1890), Weber and Sterzel (1896) and succeeding workers (Scott, 1899; Seward, 1917; Scott, 1923; etc.) emphasized that feature in comparing these plants to ferns. Seward (1917) seems to have hit upon a significant difference, however, in stating that, " though the Medullosae resemble Ferns there is an important difference between the two groups in the origin of the various plans of Medullosan stelar systems: in Ferns the leaf is the determining factor in the evolution of stelar arrangement, while in *Medullosa* the occasional interruption of a solenostele or the development of an apparently complex dictyostele are features independent of the leaf and leaf-traces ".

The structure of each of the steles in *Medullosa* has also been frequently compared to that in ferns. The protostelic nature of each stele, the primary xylem of which is composed of tracheids imbedded in parenchyma, has been likened to the structure of the vascular cylinder in some species of *Gleichenia* and *Lygodium*. This comparison may be more accurate for *Heterangium* than for *Medullosa*, although previous investigators considered each medullosan stele identical in structure with the single stele in the former genus. It was shown, however (Delevoryas, 1955), that the primary xylem of *Medullosa* is not radially symmetrical like that of *Heterangium*, but has protoxylem only on that portion of the primary wood which faces the exterior of the stem. Notwithstanding the resemblance of certain pteridosperm steles to fern steles, such superficial similarities are certainly insufficient basis on which to prove any kind of relationships. In view of the relative simplicity of such steles as are present in *Gleichenia dichotoma* and in *Heterangium*, it is quite probable that such a

type of stelar construction could easily have been attained by more than one unrelated groups of plants.

Finally, the most fern-like characteristic of the medullosae is the frond-like nature of the leaves. Before it was known that seeds were attached to certain kinds of foliage, all fern-like leaves were grouped into the Filicineae. Even at the present time, it is still impossible to determine whether certain kinds of frond compressions (which bear no reproductive structures) are leaves of ferns or of pteridosperms.

In addition to the fern characteristics that were supposed to be inherent in *Medullosa*, it was agreed by many of the earlier workers that many cycadean features also were evident. Scott (1899) saw similarity in medullosan leaf characters and cycadean leaves, in addition to regarding the root structure and presence of accessory bundles in *Medullosa* as pointing to the cycads. Seward (1917) was impressed with the cycadean nature of the secondary wood and phloem of *Medullosa*.

In a series of papers Worsdell (1896, 1898, 1900, and especially 1906) attempted to show that an actual relationship does exist between the medullosae and modern cycads. From such a type as *Medullosa stellata*, in which a hollow stelar cylinder is found, Worsdell would derive cycads by a progressive loss of centripetal secondary vascular elements, in addition to the complete loss of the central "star rings". Often in stems of certain recent cycadean genera (e.g., *Cycas*) little patches of vascular tissue within the main stele, with phloem directed toward the center, are present. Worsdell believed that this vascular tissue is all that remains of the once normal centripetal portion of a medullosan stele. In addition, Worsdell believed that the concentric vascular bundles which are occasionally observed among the cycads had their origin among some of the steles of *Medullosa*. Further evidence for medullosan ancestry which was used by Worsdell is the irregular arrangement of the bundles in the peduncle of *Stangeria*. These were interpreted as being equivalent to the sinuous steles of *Medullosa Leuckartii* which had been broken up and had lost the centripetal xylem and phloem. The anatomy of certain seedlings was also considered to show many features found among the medullosae.

The views of Worsdell were challenged by Scott (1909, 1923) who felt that a lyginopterid stem structure was more logically

the precursor of the cycadean type of anatomy. He emphasized that the medullosae are consistently polystelic, while the cycads have a monostelic stem. He furthermore found more in common between leaf traces of *Lyginopteris* and those in the Cycadaceae, than between the medullosan leaf traces and cycad vascular bundles. Arnold (1953) was inclined to agree with Scott's views, considering the theory postulated by Worsdell as being rather " indirect ".

Miss de Fraine (1912) suggested that both the views of Worsdell and Scott could be reconciled to some extent since the discovery of the genus *Sutcliffia*. She believed it to show features which were cycadean (including that of monostely) and at the same time combined characteristics of both *Medullosa* and *Heterangium*. Miss Bancroft (1914), who reviewed the problem of the origin of cycads from the pteridosperms, felt that Miss de Fraine's interpretations were the most reasonable. Delevoryas (1955), on the other hand, is of the opinion that Miss de Fraine's reasoning was not sound, since *Sutcliffia* seems to present a primitive type of medullosan construction, while it is the later Permian medullosae which seem to show cycadean affinities to the most convincing degree.

In addition, Delevoryas showed that, although the cycads possess a monostelic type of stem anatomy, an almost identical type of structure is found in such forms as *Medullosa stellata*, where the peripheral cylindrical stele was also a single unit, although probably having been derived from several separate ones phyletically. There certainly is no great step from such a stele, following a loss of the internal " star rings ", to the cycadean anatomy. Indeed, *Colpoxylon aeduense* represented just such a type in which the " star rings " had disappeared.

A fact of some strength in supporting Worsdell's ideas is the strong similarity in seed types between the medullosae and the cycads. Although the actual means of fertilization were perhaps different (sperm cells may have been formed directly within the pollen grain from which they were released [Renault, 1887; Stewart, 1951b]), seed structure was quite similar. The method of seed attachment to obviously reduced leaves in some species of *Cycas*, furthermore, seems to parallel the attachment of trigonocarp seeds on medullosan fronds.

At present there is difficulty in deriving cycadean male fructi-

fications from medullosan pollen-bearing organs, and further investigation in that line may be promising.

If there were actually two lines within the medullosae, as suggested by Stewart and Delevoryas (1952) and Delevoryas (1955), one might wonder whether the line typified by most of the Carboniferous members could have led to some later types of plant forms. That such a possibility exists must be admitted, although nothing can be definitely concluded from the fossil plants known at present. The stem anatomy of members of the Pentoxyleae described from the Mesozoic in India by Sahni (1948) has much in common with medullosan stem structure and perhaps some affinity may exist between those two groups.

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ERRATUM

On page 46, third line of caption for Fig. 2, please read "Secondary tissues are *most* abundant", instead of "Secondary tissues are not abundant".